Ecological boundaries in the context of hierarchy theory

Matthew M. Yarrow [a,*], Stanley N. Salthe [b]

[a] *Laboratorio de Modelación Ecológica, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile,
Casilla 653 Las Palmeras 3425, Ñuñoa, Santiago, Chile*
[b] *Emeritus, Biology, City University of New York Visiting Scientist, Biological Sciences, Binghamton University, Natural Systems,
42 Laurel Bank Avenue, Deposit, New York 13754, USA*

Abstract

Ecological boundaries have been described as being multiscalar or hierarchical entities. However, the concept of the ecological boundary has not been explicitly examined in the context of hierarchy theory. We explore how ecological boundaries might be envisioned as constituents of scalar hierarchical systems. Boundaries may be represented by the surfaces of constituents or as constituents themselves. Where surfaces would correspond to abrupt transition zones, boundary systems might be quite varied depending on hierarchical context. We conclude that hierarchy theory is compatible with a functional vision of ecological boundaries where functions can be largely represented as the processing or filtering of ecological signals. Furthermore, we postulate that emergent ecological boundaries that arise on a new hierarchical level may contribute to the overconnectedness of mature ecosystems. Nevertheless, a thermodynamic approach to the emergence and development of boundary systems does indicate that in many situations, ecological boundaries would persist in time by contributing to the energy production of higher hierarchical levels.
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1. Introduction

The study of ecological boundaries as functionally active components of landscape mosaics has come into its own. A 2003 issue of *BioScience* included several papers dedicated to theoretical and empirical considerations in the study of boundary systems and represents the latest comprehensive revision within this sub-discipline. In an attempt to incorporate areas of ecological boundary research that are often viewed as unrelated (due to differences in scale or study systems), Cadenasso et al. (2003b) piece together a very general theoretic framework. The authors subsequently demonstrate that model templates and eventually working models can be derived from this generalized framework. However, because the framework is painted in such inclusive strokes, it does little to guide the formulation of hypotheses or the scale(s) on which to address research questions.

Several authors have examined ecotones or ecological boundaries using a hierarchical approach (Gosz, 1993; Kolasa and Zalewski, 1995; Peters et al., 2006). However, there has been a tendency to selected organizational levels *a priori* for specific study systems, limiting the generality of the analysis. Additionally, we suggest that hierarchy theory has not yet been fully explored as a tool for examining ecological boundaries. In this paper, ecological boundaries are placed in the context of hierarchy theory, which provides a slightly less general, but much richer, theoretical framework which can serve as an invaluable guide in structuring empirical studies.

2. Background

2.1. The State of Boundary Studies

The study of ecological boundaries is an old and haphazardly organized sub-discipline of ecology. Ecotones were defined by Clements as a zone of 'tension' between two vegetation units or large-scale communities (1905). Ecologists who used the ecotone concept from the 1930s through the 1960s worked in a somewhat isolated manner at distinct scales (forest edges to continental biomes) (Risser, 1995). The development of landscape ecology brought the conceptualization that boundaries (along with patches) are the essential structural/functional components of landscape mosaics (Cadenasso et al., 2003a). Holland (1988) viewed ecotones as the transition zones between adjacent

* Corresponding author.
  E-mail address: matiasyarrow@yahoo.com (M.M. Yarrow).

ecological systems, in effect supporting a functional/systemic approach to ecotone studies. Currently, boundaries are often viewed as dynamic, multidimensional transition zones that exhibit greater internal heterogeneity than adjacent ecological systems (Cadenasso et al., 2003a; Peters et al., 2006).

Recent papers on ecological boundaries have regularly examined these systems from the perspective of landscape ecology (Cadenasso et al., 2003a; Strayer et al., 2003; Laurance et al., 2001). The power of this approach is that it examines the spatial heterogeneity of boundaries imbedded in landscapes and it provides tools for the structural characterization of boundaries at different scales. However, as several authors acknowledge, in landscape ecology much of the attention has been given to spatial pattern analysis (Wu and David, 2002; Turner, 2005). Although ecosystem processes are being considered more often in the context of landscape ecology, an explicitly functional approach to studying boundaries could deepen understanding of the role of these systems in landscapes.

The functionality of boundary systems has been described in different ways by different authors (see Table 1). Forman and Moore (1992) described boundary functioning in terms of filters, barriers, conduits, sources, sinks, and habitats. It is interesting to note the use of both population ecology concepts (habitat, source, sink) and functional/engineering concepts (filter, conduit, barrier). Strayer et al. (2003) used a set of functional concepts commonly used in physics to describe the behavior of wave signals: transmission (partial), transformation, absorption, reflection, amplification, and neutral (no effect). These functional descriptors do not make reference to the hierarchy of ecological organization (individual, population, community, ecosystem) or to the spatial–temporal scale of the process in question, and are, therefore, appropriately universal. In addition, these functions can be reproduced by a filter, emphasizing the importance of how the frequency and amplitude of a signal change with its passage through a filter. This observation lends itself neatly to the theory of ecological hierarchies, where each component has a characteristic cycle time of endogenously driven behavior and thus transmits signal of a characteristic frequency (Allen and Starr, 1982).

2.2. Boundaries, Delimitation, and Epistemological Concerns

A clarifying prelude to the following examination of hierarchy theory and ecological boundaries is needed. Several confounding issues arise when discussing theoretical and often abstract concepts and their utility for informing the study of tangible entities. First, it is important to reiterate that the perception of ecological concepts as ontological entities is problematic and has been viewed as an obstacle in ecological theory (Jax, 2006). Therefore, theoretical concepts are viewed here as constructs useful for ordering our thinking about the natural world. An ecological boundary is one such concept; to move from this theoretical realm to the empirical, an operational definition of the ecological boundary in question must be formulated and the boundary limits must be established in the field (Jax, 2006; Fagan et al., 2003).

Because ecological boundaries and scale hierarchies can be examined using either a structural or functional approach, care is required in order to avoid confusing these often distinct theoretical frameworks. That said, ecology benefits from the comparison and integration of structural and functional approaches (Turner, 2005). We use the term "function" to refer to groupings of several processes viewed at the level of a subsystem or system (Jax, 2005). Several authors emphasize the functional aspects of hierarchical systems, choosing to examine process rates (Allen and Hoekstra, 1992; Allen and Starr, 1982). Likewise, many authors have noted the importance of ecological boundaries as functional components in landscapes (Cadenasso et al., 2003a; Peters et al., 2006). Thus, it seems that a focus on the process rates and signal processing characteristics of ecological boundaries is well placed. On the other hand, Salthe (1985) emphasizes the role of structural units as parts of hierarchical systems. Such units have boundaries that constrain what states they can assume and what processes occur within. Can these boundaries themselves be thought of as ecological units? Ultimately the answer is yes, but frequently one must look to a lower hierarchical level to see such boundaries as entities that are truly distinct from their surroundings (Salthe, 1985). A structural approach is conceptually in line with the majority of edge detections methods currently used in boundary studies (Fagan et al., 2003).

A further issue relates to how we understand structural and functional change across spatial scales. As an analytic tool, hierarchy theory searches for scale breaks in structural components or processes of complex systems (Wu, 2004). Patterns in spatial heterogeneity are often distinct at different scales. Furthermore, different structuring processes can emerge at different scales (Peterson, 2000). These observations support the view that complex systems present a certain hierarchical modularity whereby discrete levels can be identified and used in structuring experimental design and conceptual understanding. On the other hand, the application of fractal methods in ecology has supported the idea that ecological units can present self-similarity over a range of scales. This approach simplifies the description of complex forms, resolves the problem of scaling-up or scaling-down through the use of power laws, and indicates that certain processes may be relevant over a large swath of the scale continuum (Halley et al., 2004). The ecological world is probably not either truly fractal or inherently hierarchical in nature, and so it falls on the ecologist to choose theoretical and analytical tools according to the system under study (Halley et al., 2004). Ecological boundaries are often defined as areas that differ significantly from their neighboring systems in terms of spatial scale, structural attributes, and process rates (Cadenasso et al., 2003a). In other words, boundaries and neighboring systems can be seen as discrete ecological units – indicating that hierarchical approach is appropriate.

2.3. Previous Hierarchical Perspectives of Ecological Boundaries

Hierarchical concepts began to have resonance with ecologists as the fundamental importance of scale became widely recognized in the late 1970s and 1980s (O'Neill et al., 1989).

Table 1
Properties and functions of the ecological boundary and related concepts

	Property or Function
Surfaces (Allen and Starr, 1982)	**Integration of signals from lower levels** **Filter** Surfaces can smooth incoming signals, affect their meaning, and even block communication between holons of different scales. **Isolation from disturbance (stability)** Surfaces can isolate their internal processes from damaging signals. **Directionality of processes and signals** Strong internal reactions occur parallel to surfaces. Surfaces can function as conduits.
Ecological boundaries (Strayer et al., 2003; Kolasa and Zalewski, 1995)	**Transmission (partial) of signal** Boundary filters signal during passage. **Transformation** Signal is transformed from one type of material, information, or energy to another. **Reflection** A signal enters the boundary but is reflected back to original system (feedback function). Can also be viewed as a barrier function. **Amplification** A signal is amplified by boundary; often occurs when processes are accelerated. **Habitat** Boundaries can provide habitat for organisms. **Conduits** Linear forms function as corridors in landscapes.
Thermodynamic gradients (Müller, 1998)	**Driving force of ecosystem processes** Ecosystem dynamics is thus dependent on patterns of gradient formation and degradation. **Consequence of dissipative self-organization** The level of a systems' self-organization can be evaluated by concentration of internal gradients. **Asymmetric interaction** In hierarchy theory gradients are scaled objects and thus interact asymmetrically across scales. **Functionality is scale-dependent** Internal gradients make up holons and underlie ecosystem dynamics and development. External gradients provide energy flow to system.

Gosz and Sharpe (1989) consider ecological boundaries and the gradients of environmental variables that constrain boundary function at the biome level. They recognize that constraints are scale-dependent and that at each level one or more gradients of varying steepness give rise to changes in vegetation structure and system processes. They suggest that quantification of these constraint gradients provides: 'a powerful tool for analyzing the control of system processes at different scales from between geographic regions to between microsites within local habitats'. In his 1993 paper, Gosz describes the ecotone hierarchy found at biome transition zones. At each of the four fixed levels in the hierarchy Gosz lists possible constraints. Interestingly, Gosz states that as scale decreases, the number of constraints increases and postulates that the rapid and unpredictable behavior of small-scale ecotones is due to the complex interactions of an increased constraint set. This is, however, a debatable assertion. Salthe's (1985) principle of nontransivity of constraints reveals that constraints are not passed from scale to scale and do not interact as such. Instead, rapid change is formally expected at smaller spatiotemporal scales in comparison with larger ones.

Peters et al. (2006) continue in the vein of Gosz (1993), describing "biotic transitions" as occurring at set organizational levels that are hierarchically ordered. Thus boundaries occur between root or leaf patches, plant patches, assemblage patches, and as structural elements of landscape mosaics. Under this conceptual model, boundaries only occur between ecological units that are at the same organizational level and spatial scale, implying that the boundaries themselves belong to the same hierarchical level as neighboring systems. We attempt to show that the hierarchical analysis of boundaries does not have to consider all involved systems as ecological units at the same hierarchical level.

Kolasa and Zalewski (1995) put the exogenous and endogenous factors that control the boundary between fluvial and terrestrial systems in a hierarchy. They also discuss problems associated with the study of boundary dynamics in the context of arbitrarily defined adjacent ecosystems. If a research question explicitly considers between-system boundaries then these should correspond to multiple ecological discontinuities. According to the authors, discontinuities that appear inside a study system should be considered as part of the 'fabric of the larger system' and accorded a lesser status than those that, because they co-occur there, mark system boundaries (Kolasa and Zalewski, 1995).

Although it has often not specifically addressed ecological boundaries (but see Peters et al., 2006), the hierarchical patch dynamics model has proved valuable in the study of landscape dynamics at different spatial and temporal scales (Kotliar and Wiens, 1990; Wu and Loucks, 1995). Essentially, ecological systems are viewed as spatially explicit nested hierar-

chies of patches (Wu, 1999). One weakness of the patch–matrix landscape model (upon which the hierarchical patch dynamics model is based) is that ecological boundaries are invariably approached as linear elements, when in fact these transition zones are three-dimensional and can be structurally complex (McGarigal and Cushman, 2005; Cadenasso et al., 2003a). Hierarchy theory allows us to consider ecological boundaries on their own characteristic scalar level and provides guidance as to how they might then be integrated into larger ecological systems.

2.4. Hierarchy Theory

Ecological systems were characterized by Weinberg (1975) as middle-number systems, where non-random interactions between an intermediate number of parts gives rise to behavioral complexity and analytical intractability (Salthe, 1985; O'Neill et al., 1989). Hierarchy theory provides a general framework for dealing with organized complexity such that ecological systems can be handled as small-number systems (O'Neill et al., 1986). The near-decomposability of ecosystems means that they can be divided into interacting subsystems at different hierarchical levels without significant loss of information (Allen and Starr, 1982; Wu, 1999).

Each hierarchical level has a characteristic behavioral frequency that is inversely related to its position in the hierarchy.[1] There is a fundamental asymmetry between hierarchical levels. Higher levels limit the behavior of lower levels by imposing constraints or boundary conditions, while lower levels constrain higher levels through initiating conditions or biotic potential—the availability of biotic components that catalyze certain ecological processes (Salthe, 1985; O'Neill et al., 1989). Slower, constraining levels integrate the dynamics (or more precisely the emitted signals) of lower levels. These integrated signals are averaged or lagged so that they minimally affect the constraining level (Allen and Starr, 1982). As mentioned previously, levels can be thought of as corresponding to scale breaks in a vertical scalar continuum. They are, therefore, abstract concepts that depend on which ecological phenomena are being investigated. Hierarchical subsystems can be viewed as relatively discrete entities at any one level (which may be seen as continuous in a horizontal plane) (Salthe, 1985). Subsystemic entities are referred to as constituents, unless they are specifically considered to be functional parts of a process under study (Salthe, 1985).

Signals can be thought of as strings of energy, materials, or information that move between components; they only have meaning when viewed in the context of the emitting component or after they have been 'translated' by a receiving component (Allen and Starr, 1982). It is important to note that constituents at different hierarchical levels cannot interact in the common sense of the word because the frequency of their characteristic behavior is separated by at least one order of magnitude. Thus, there is a 'nontransivity' of information and dynamics between levels that impedes communication and implies that levels affect each other indirectly, through constraints (Salthe, 1985).

Subsystems at the same hierarchical level can theoretically interact in an unhindered fashion because their endogenous behavior occurs at similar frequencies. However, the extent of such interaction is questioned by several authors. Hári and Müller (2000) postulate that horizontal interactions have: "minor significance for the system's behavior and development". Wu (1999) writes that the principle of near-decomposability applies both in vertical and horizontal directions. In this view, subsystems at a given level will have greater effects on interactions between their components as compared to interaction with neighboring subsystems. Nevertheless, these subsystems then become the components of systems at higher hierarchical levels, implying the importance of horizontal interaction in providing identity and cohesiveness to higher level entities (Wu, 1999).

A distinction should be made between nested and non-nested hierarchies. The apical system in a nested hierarchy contains the "sum of the substance and interactions" of lower level constituents in a system, whereas subsystems in non-nested hierarchies lie outside their constraining levels (Allen and Starr, 1982). Application of hierarchy theory in ecosystem ecology has focused largely on nested hierarchies (Salthe, 1985; O'Neill et al., 1986). In a non-nested hierarchy, the higher level subsystems can constrain the lower level subsystems but do not physically contain them. In such cases it is readily seen that, temporally, slow dynamics will regulate faster ones, and so the cogent moments are virtually nested in a formal sense (Salthe, 1985).

The concept of surfaces is another component of hierarchy theory relevant to ecological boundaries. According to Allen and Starr (1982), surfaces are the natural breaking points in systems, and they occur at places where the gradient in the time constant of a subsystem's characteristic behavior becomes very steep as the observer increases the size of the observation window. The thermocline that forms in some lakes along a steep temperature gradient is an example of a surface. The thermocline exhibits self-reinforcing behavior that favors its persistence in time and imparts stability to the system of which it is a part (Allen and Starr, 1982). Additional surface properties and functions appear in Table 1.

2.5. Thermodynamics, Energy Gradients, and Dissipative Structures

Thermodynamic considerations can inform the topic at hand. The second law of thermodynamics (the tendency of the Universe to move toward thermodynamic equilibrium) provides a final cause for the structure and dynamics seen in ecological

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[1] Also called endogenous cycle time—the time a system takes to complete a cycle of characteristic behavior (e.g., the generation time for a population). The relaxation time is the time a system takes to return to equilibrium behavior after being perturbed by an exogenous signal; it can be used as an alterative criterion for establishing hierarchical levels (Allen and Starr, 1982). Salthe (1985) has proposed a distinct but compatible way to view characteristic frequencies: the cogent moment. Entities at different levels would experience time at different temporal scales. This approach obviates the need to suppose the system to be at equilibrium.

systems (Salthe, 2004a). Energy gradients are multiscalar and ubiquitous. Steep energy gradients spontaneously give rise to dissipative structures which facilitate the production of entropy during their dissipation (Salthe, 2005). Energy is used by dissipative systems to self-organize, and it has been postulated that living systems are perhaps the most effective and stable entropy producers, an idea that sheds light on their origin and historical resilience (Kay, 2000; Salthe, 2004a). Additionally, increases in the magnitude of internal cycling or in the number of hierarchical levels in an ecological system improve the system's entropy degradation and should be favored as a system matures (Kay, 2000; Salthe, 2004a).

Müller (1998) proposes that gradients be seen as more than just existing energy differentials. Gradients are differences between both structural components and energetic or material concentrations within ecosystems; ecosystem processes are thus the 'reactions which build up or degrade structural gradients' (Müller, 1998). For Müller, gradients are both the impetus and result of dissipative self-organization. This makes more sense when gradients are viewed in hierarchical terms. According to Müller (1998), the production of a series of hierarchically ordered internal gradients allows self-organizing systems to deal with and process powerful external gradients. In essence, Müller conceptually maps hierarchical subsystems to dissipative gradients and views the resulting ecosystems as "systems of gradients".

There is congruence between gradient delineation and that of subsystem surfaces and ecological boundaries: all can involve a spatial comparison of state variables (structural perspective) or a spatial–temporal examination of process rates (functional perspective) (O'Neill et al., 1986; Müller, 1998). However, there is not a one-to-one mapping between Müller's gradient concept and the ecological boundary concept. Perhaps the best way to understand ecological boundaries in these terms is that they would occur where numerous gradients of similar spatial or temporal scales coincide. The resulting boundaries would be conceptually akin to set of dissipative structures distinct from adjacent systems and of an elevated functionality. One could hypothesize that self-organizing systems, which create gradients through the degradation of other gradients, could ultimately exert control over the location and contrast of their boundary through the process of gradient creation. In the end, though, the all-inclusiveness of Müller gradients is problematic. From our perspective, gradients give rise to dissipative structures which can efficiently process such gradients. It is not the gradients which impart structure to ecological systems; they are essential affordances for such structure.

Three concepts relating to ecological boundaries have been discussed thus far. In order to avoid confusion in the remaining sections, the following working definitions will be used: (1) thermodynamic gradients are viewed as components of ecological systems that are created and degraded as a system moves toward the attractor of dissipative self-organization; (2) surfaces are portions of the scale gradient in a hierarchy that are so steep they appear as steps, surfaces represent the places where a system is logically decomposed; (3) ecological boundaries are transition zones between ecological systems or patches (Müller, 1998;

Allen and Starr, 1982; Cadenasso et al., 2003a,b). It is probable that to some degree when these three concepts are delineated in material systems, they will correspond in space and time.

3. Hierarchical Boundaries: Conceptual Models

It is proposed that placing the ecological boundary concept in a hierarchical framework leads to insight about scale relations and the process dynamics of boundaries. Furthermore, a hierarchical perspective can aid the development of hypotheses and the selection of appropriate conceptual models to guide empirical research. A basic triadic hierarchical structure is sufficient to encompass most ecological questions, essentially balancing comprehensiveness and conciseness (Salthe, 1985). The focal level is set at 0 and receives constraints from level +1, itself constraining level −1 (Fig. 1). The lower levels pass information up the hierarchy in the form of initiating conditions or biotic potential. Interactions are possible between components of the same level—indeed only within a hierarchical level can interactions between components be seen as truly dynamic. As a signal passes a surface, it is filtered and converted into a message on a scale similar to the endogenous cycle time of the hierarchical level in question. As a general guideline, hierarchical levels that are separated by an order of magnitude or more in their endogenous cycle rates would be unable to interact directly (Salthe, 2004a). Because this decoupling of the behavior on different hierarchical levels allows a system to avoid chaotic dynamics and become more effective its production of entropy, it will be favored in thermodynamic sense.

3.1. Ecological Boundaries as Surfaces

Perhaps the simplest way to view ecological boundaries in the context of the hierarchical system model are as the surfaces of constituents. Both surfaces and boundaries can be located in real-
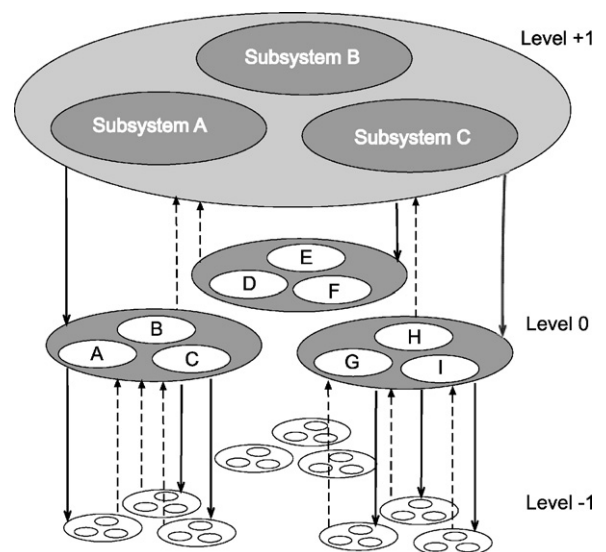

Fig. 1. Schematic of a nested hierarchy. A number of discrete constituents occur on any given hierarchical level. Constraints are indicated by solid arrows; initiating conditions or biological potential are indicated by dotted arrows.
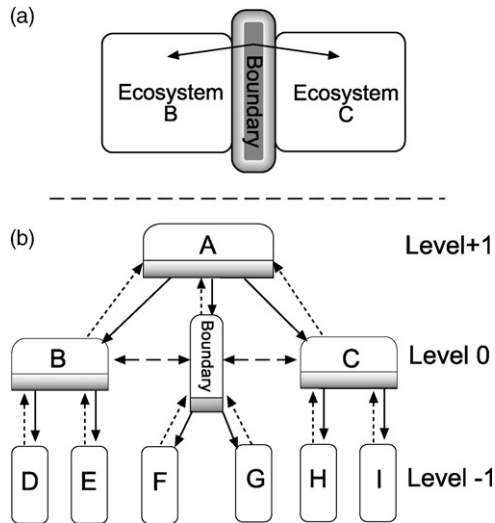
Fig. 2. A boundary as a subsystem on the focal level of a nested system; (a) as a simple conceptual model; (b) as a hierarchical model. Those surfaces that provide maximum filtering of signals are represented by shaded rectangles.

world systems through the measurement of the rate of change in process frequencies across space and time. Boundaries and surfaces of ecological consequence will be aligned along numerous process scale breaks, effectively grouping certain ecosystem functions in time and space. Surfaces can function as filters; such filters are graphically represented in Fig. 2 as facing the lower level constituents. This represents the asymmetrical nature of signal exchange across a surface: filtering occurs as signals are integrated from lower hierarchical levels but a constituent's characteristic behavior can be transmitted to neighbors on the same level without major signal modification (Allen and Starr, 1982; Hári and Müller, 2000; Lemke, 2000). In the words of Allen and Starr (1982), subsystems at the same hierarchical level have the same filter, and thus information can be exchanged without alteration.

Ecological boundaries conceptualized as surfaces would correspond to those boundaries that do not have distinct state variables and internal behavior at the scale of focus. In other words, they would likely be linear-shaped boundaries having steep gradients and the capacity to modify signals passing vertically from one constituent to another. Lacking discernable internal processes at the scale of interest, this type of boundary would probably not transform signals from one type to another but rather filter the magnitude and frequency of in-coming signals from lower levels. Furthermore, this type of boundary would allow the passage of signals laterally with minimal filtering. Thus, knowing the process rates of adjacent systems would be critical for they would determine if the boundary would meaningfully alter incoming signals. An example of a surface-type boundary in a real-world system is the edge between forest and pasture patches where human activities maintain a steep environmental gradient (Murcia, 1995). The behavioral frequency of a managed pasture (life cycles of principal species, nutrient cycles, herbivory stress and release) could reasonably be seen as significantly higher than a mature forest and thus be considered as occurring on a lower level. A boundary of this type would

filter signals (wind-dispersed seeds from the pasture are filtered by the boundary as they enter the forest) but not transform the signal type (seed species composition remains the same). On the other hand, the boundary between two forest patches of different biotic composition, might allow for the transfer of materials or information with little change in the signal.

3.2. Ecological Boundaries as Subsystems in a Hierarchy

If at the scale of focus, a boundary emerges as subsystem, with its own internal structure and characteristic rate of endogenous behavior, then it can be conceptualized as a distinct subsystem in a hierarchical system model. There are several hierarchical configurations possible with different ramifications for boundary function.

3.3. Boundary on Same Level as Adjacent Systems

The case where an ecological boundary has an endogenous cycle time that is close to those of adjacent systems is represented visually in Fig. 2. The horizontal geometry of this model is initially appealing because of the many instances of similar-sized patches forming boundaries in landscape mosaics. Hierarchy theory can suggest certain dynamics for this conceptual model, but it should be noted that hierarchy theory emphasizes inter-level dynamics. The patterns of constraint that are transmitted between levels are what allows ecologist to make predictions (O'Neill et al., 1989).

Because we are discussing the ecological boundary as a subsystem on the same level of a scalar hierarchy as its adjacent systems, it is reasonable to think that such a boundary would be truly three-dimensional at the scale of focus (as opposed to a sharp, linear transition zone). This draws attention to the similarity between this model and the ecocline concept. As described by Van der Maarel (1990), an ecocline is 'a gradient zone which is relatively heterogeneous but environmentally stable'. Given that the boundary in this case is viewed as a subsystem with its own state variables and emergent properties, the heterogeneity described by van der Maarel is appropriate. An example might be the transitional community of stunted trees and shrubs near treeline as a boundary system between montane rainforest and alpine tundra. The primary underlying gradient (or higher level constraint) may be average annual temperature which varies with the glaciation cycle (Attrill and Rundle, 2002). On a somewhat smaller scale, the ecotone between forest and field has many species adapted to its special properties and not found on either side. In Northern Hemisphere systems the garlic mustard (*Alliaria petiolata*) is a well-known example (Booth et al., 2003).

The relative stability of the ecocline-like boundary system might be explained in several ways. First, on an ontological level, the components on a given hierarchical level that interact strongly are likely to be grouped into a subsystem, leaving a set of weak interactions between subsystems (O'Neill et al., 1986). Thus, although there is potential for strong interaction between subsystems at a given hierarchical level, common delineation

criteria preclude this type of dynamic. Second, we have seen that surfaces only minimally filter signals between constituents on the same hierarchical level (Allen and Starr, 1982). If the signals (materials or information) that pass through a boundary system are of a regularly processed type, then the boundary is likely to remain fairly stable, i.e., the signals do not push the subsystem beyond its 'constraint envelopes' (O'Neill et al., 1989). Third, if a gradient underlying the boundary system imparts certain directionality to signals, this might be seen as an obstacle to feedback loops which could disrupt a metastable state. Fourth, the boundary system and adjacent subsystems all operate under the constraints imposed by entities on the +1 level. Such constraints can limit strong interactions or retard the emergence of chaotic behavior.

On the other hand, a boundary system at the same hierarchical level as adjacent systems presents a distinct possibility of feedback loops and chaotic behavior. As a functioning system, the boundary will be able to process incoming signals, potentially altering their frequency, content, and strength, as well as introducing time lags between their reception and release. If the connectivity between the boundary and adjacent systems is high, and boundary signal processing introduces irregularity, it is probable that chaotic dynamics will emerge. Essentially, as processes at the focal scale become mutually interfering, turbulence ensues (Salthe, 2004a). Thus, given strong interactions at the focal level, this conceptual model will be unstable.

It should be possible through the examination of ecological perturbation to reconcile the two visions presented above of a boundary system at the same level as its adjacent systems. A perturbation is an uncontrolled and unpredictable signal that comes from outside the study system (O'Neill et al., 1986). A perturbation will most powerfully affect those constituents with scales similar to, or (more destructively) smaller than, the perturbation signal. Incorporation describes the process whereby a perturbation that occurs frequently at a particular scale begins to form a common "identity" with the constituents on that scale (Allen and Starr, 1982). In other words, the perturbed subsystem adapts to the perturbation cycle, eventually becoming dependent on it (as in the case of fire-adapted grasslands). Thus the boundary could be perturbed or pass on disruptive signals to neighboring subsystems (which would be seen as chaotic behavior at the focal level), but eventually such signals can become incorporated and the involved subsystem will again appear stable.

3.4. Boundary Interpolated Between Adjacent Systems on Different Hierarchical Levels

Fig. 3a is a graphical representation of the situation where a boundary system separates two ecosystems showing different endogenous cycle rates. Fig. 3b more explicitly shows the position of the boundary in a hierarchical model and how it splits the difference in scale between level +1 and level 0. The importance of a decrease in rate differentials between levels with the insertion of a boundary system is evident in Salthe's (2004) postulation that hierarchical levels are separated by approximately orders of magnitude in their endogenous cycle rates thereby avoiding interference between processes on different scales.
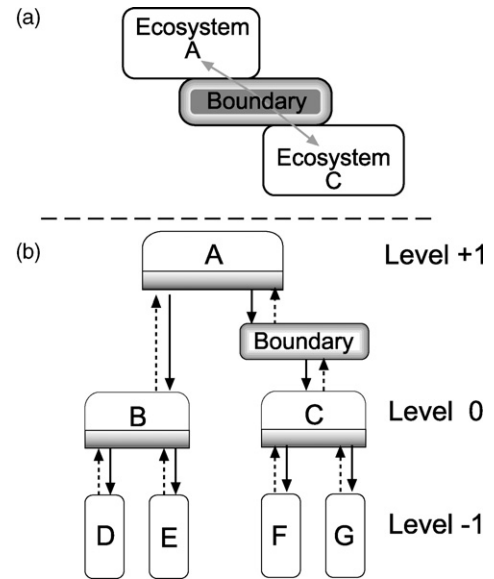

Fig. 3. A boundary as a component occurring on an interpolated level in a nested system; (a) as a simple conceptual model; (b) as a hierarchical model.

Because the order of magnitude criterion is not met in the case of the boundary system, low frequency signals from the +1 level are unable to act as constraints and instead are incorporated into the processes operating at the level of the boundary. In fact, signals received from level +1 are more dynamic and potentially more forceful than these same signals at level 0. The signals emitted by the boundary subsystem are received by level 0, and again, instead of functioning as slow-moving forcing functions or as constant boundary conditions, these signals are close enough to the behavioral frequency of level 0 that they can potentially act as powerful drivers. The boundary in Fig. 3 will also act as a filter to the signals originating in level 0, thereby facilitating their passage to level +1. In the absence of an interpolated boundary, this would not occur, as all dynamical behavior at level 0 would be lost at level +1 (Salthe, 1985). In fact, the relationship between the boundary and levels 0 and +1 may exhibit complex behavior that would complicate prediction of flows within the system.

If we consider that a boundary lies between two levels and exhibits endogenous cycle rates less than an order of magnitude from its neighbors then the following hypotheses might be put forth:

(1) The signals received from constituents on upper and lower levels do not serve primarily as constraints to the boundary but rather as drivers that more directly influence boundary-level dynamics.
(2) This intermediate position of the boundary between two established levels will be relatively short-lived (as judged by the cogent moment of the boundary system). The reason is that this configuration is likely to produce chaotic behavior until levels have become separated by more than an order of magnitude.
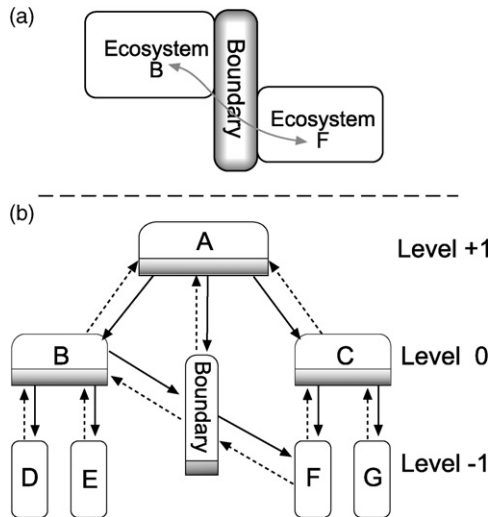(3) Signals from constituents on level 0 or level +1 may be modified by their passage through the boundary and thus

Fig. 4. A boundary between different stems in a nested hierarchical system; (a) as a simple conceptual model; (b) as a hierarchical model.
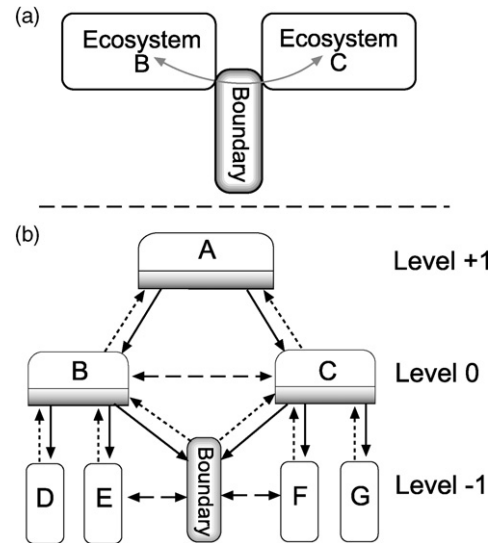

Fig. 5. A boundary as a subsystem on an inferior level as compared to the adjacent systems; (a) as a simple conceptual model; (b) as a hierarchical model.

strong communication (probably temporally limited) can take place.

3.5. A Boundary Between Systems on Different Stems

Fig. 4 shows a situation similar to Fig. 3: two ecosystems with distinct endogenous cycle times, their signals mediated by a boundary system. The difference lies in that the two ecosystems are on different stems in the hierarchy. In Fig. 4a, it appears that we are dealing with a non-nested hierarchy. However, in order to better understand system dynamics, it is suggested that the model be expanded to include constituents on a hierarchical level that constrains all subsystems under consideration—in this case level +1. This is important because it might appear to an observer at the focal level that the boundary is mediating certain similarities found in ecosystems B and F when in fact such patterns would be more parsimoniously described by the constraining effect of a common apical subsystem. The boundary system serves to split the vertical difference in scale between levels 0 and −1. As in the case of Fig. 3, signals from ecosystems B and F received by the boundary are relatively close to its internal behavioral frequency and can affect its dynamics in unpredictable ways. In Fig. 4, it is expected that the boundary will allow for greater interaction between the two ecosystems than would be the case with no boundary system. However, it is unlikely that such interactions would be strong enough to lead to chaotic behavior, as might be the case in Fig. 3. In addition, we might expect that the common constraining level would impose certain limits on boundary function.

An example of the model in Fig. 4 might be the case of a river and terrestrial ecosystem separated by a riparian boundary system. The river system would exhibit relatively fast behavior (in terms of the life cycles of biotic components and nutrient cycling) and might be said to be constrained by watershed geomorphology (as would the terrestrial system). The riparian system would be influenced by the high frequency hydrology of the river system, but its internal structure would provide the

basis for other slower processes (Naiman and Décamps, 1997). The slower terrestrial system could emit signals in the form of sediment or nutrient fluxes which would be filtered and altered before reaching the river. Flood events could affect terrestrial systems, but their frequency and intensity would be mediated by the riparian system.

3.6. The Boundary as a Subsystem on an Inferior Level Compared to the Adjacent Systems

Finally, the boundary might be considered as a subsystem on an inferior level to its adjacent systems not entirely contained by either of them (Fig. 5). In this case, the boundary would exhibit endogenous cycle rates at least an order of magnitude greater than its neighboring systems. As viewed from the focal level, the boundary system would appear as an abrupt transition zone. A boundary system in this hierarchical configuration would not interact as such with its neighboring systems because their system-level behavior would in comparison be extremely slow. Rather the boundary would be heavily constrained by these two systems. The usual functions attributed to ecological boundaries would not be applicable in this context, as dynamic interactions at the focal level would not involve the boundary system. However, the boundary might interact with the components of its neighboring subsystems—essentially providing a more direct signal pathway that would not involve the integration of subsystem dynamics at the focal level. Thus, the boundary would be wedged between two large, relatively stable systems that would restrict its behavior (for example, physical boundary growth would be restricted). However, the boundary might be seen as playing a dynamical role in the local subsystems of its larger neighbors. One might consider the halocline in a large estuarine system. The dynamics of the large bodies of fresh and salt water would place major constraints on the location and dynamics of the halocline. The halocline, in turn, interacts

locally with its neighbors, affecting species composition in its vicinity.

4. Discussion

4.1. Boundaries as Hierarchical Signal Processors

Strayer et al. (2003) characterized boundary function as the change a boundary causes in incoming signals. The above examination of ecological boundaries in the context of hierarchical systems also emphasizes the fact that boundaries are signal processors. Furthermore, the frequency of incoming signals and the ability of the boundary to process them are dependent on the position of the boundary system in a hierarchy. Several conclusions can be drawn. First, boundaries that have fast process rates may not be able to dynamically interact with large, slow neighboring systems, and thus the functional role of boundaries should be seen as context-dependent. Second, viewing boundaries as signal processors means that a thorough search for functional mechanisms and a thorough description of boundary structure are not necessary when examining the role of boundaries at higher scales. Third, the concept of signal processors appears to be general enough to be applicable at numerous hierarchical levels, although the underlying processes may be scale-dependent. If a set of general descriptors for boundary functions based on signal processing (perhaps borrowing from the field of electrical engineering) could be formulated, it could facilitate a relatively rapid functional characterization of boundaries in landscape mosaics and might be used as an important management tool. Finally, an understanding of the way boundaries and other subsystems in a hierarchy process signals can give insights as to how best scale-up or scale-down the patterns or dynamics observed at a focal scale (Peterson, 2000).

4.2. Ecosystem Development and the Emergence of Ecological Boundaries

Previous sections have examined ecological boundaries in specific hierarchical contexts. This has brought up questions of how boundaries emerge, persist and develop in time, and even-

tually breakdown or disappear. Some authors have downplayed the usefulness of hierarchy theory when a system is reorganizing or going through structural breakdown (O'Neill et al., 1989; Hári and Müller, 2000). However, a coupling between hierarchy and thermodynamic theory can guide conceptual advances in understanding ecological boundary development. The literature on ecosystem development and their self-organizing and emergent properties has largely viewed systems as discrete entities with limited interaction with adjacent systems. On the other hand, boundary studies are often synchronic—placing the most emphasis on contextual and spatial aspects of boundary systems. In this context, the current section is best viewed as a brief treatment of a topic requiring a more exhaustive analysis and synthesis.

In order to deal with the complexity of simultaneously considering synchronic and diachronic aspects of ecological boundary development and emergence we look to the four types of Aristotelean causality: (1) material, (2) efficient, (3) formal and (4) final (Salthe, 2004b). As Ulanowicz (1990) has mentioned, formal and, especially, final causalities were filtered from scientific discourse during the age of Enlightenment. Nevertheless, system ecologists now employ terms such as "goal functions" or "attractors" when discussing the development of complex, nonlinear systems; these concepts can be seen as final causes (Jørgensen et al., 2000; Nielsen, 2000). Table 2 creates a conceptual matrix where the four forms of Aristotelean causality are applied to the main flows that occur within and between ecosystems. Because boundary systems are often envisioned as mediating these flows, this table acts as a starting point to begin teasing apart the hows and whys of ecological boundary development. Final causes to ecosystem development tend to occur at higher levels of organization (Ulanowicz, 2004). Thus, in the case of boundaries categorized as occupying lower positions in a hierarchy as compared to adjacent systems, we see that the "pull" toward development will likely come from these systems. A climax forest may represent the principal attractor at a forest-field boundary due to its position in a scale hierarchy. On the other hand, efficient causes to boundary development often occur at the focal level as perturbations. Thus a boundary might be pushed in a certain direction by the activity of a keystone species like beavers,

Table 2
Aristotelean causality in ecological boundary systems

Aristotelean causality	Types of ecosystem flows		
	Information	Material	Energy
Synchronic			
Material	Seed bank, genetic diversity of populations	Nutrients, substrate	Solar radiation, biomass
Formal	Species interactions, patterns of landscape flows (i.e., prevailing wind direction)	Structural differences between neighboring systems, abiotic gradients	Differences in energy capture, flow rates, and entropy production between neighboring systems
Diachronic			
Efficient	Arrival of propagules from neighboring systems, activities of key species	Physical disturbance patterns: floods, wind, landslide, human	Solar radiation changes and photoperiod, import of biomass
Final	Accumulation of genetic diversity, foodweb complexity, tight nutrient cycles, Ascendency	Creation of dissipative structures (Schneider and Kay, 1994)	Maximum Entropy production, 2nd law of thermodynamics, maximum energy storage (Jørgensen et al., 2000)

The entries in this table represent a selection of factors, processes, or attractors that are relevant to the emergence and development of boundary systems.

or intense fluxes of material occurring as floods, wind storms or land slides. Material causes often operate on lower hierarchical levels as "initiating conditions" (Salthe, 2004a). Circular or mutual causality (also discussed by Aristotle and often viewed today as obfuscating or undermining simple lineal cause-and-effect) should be noted due its relevance to boundary dynamics. Mutual causality is associated with feedback loops and autocatalytic loops (Ulanowicz, 2004). Signals moving through the boundary can act as efficient cause to changes in the neighboring systems; such changes can elicit flows back through the boundary, creating a mutual causal situation in which the boundary mediates the signals. One example is a boundary capturing atmospheric deposition of nutrients (Weathers et al., 2001), eliciting more biomass production in the adjacent forest system, and perhaps ultimately providing for greater export of biomass toward the neighboring grassland.

A thermodynamic perspective underlies an understanding of changes that occur in a hierarchical system over a cycle of ecosystem development and senescence (Holling, 1992; Salthe, 1993, 2004a,b). An open system that is exposed to energy gradients across its boundary will use this energy to create dissipative structure, thereby moving further away from thermodynamic equilibrium. The Second Law of thermodynamics represents the final cause for an ecosystem's tendency to maximize entropy production through energy-dissipating structures (Schneider and Kay, 1994). Other thermodynamic orientors have been proposed to describe certain structural or dynamical aspects of mature systems toward which immature systems tend to develop. Worth mentioning are Odum's Maximum Power Principle (Odum and Pinkerton, 1955) and Jorgensen's energy storage hypothesis (Jørgensen and Mejer, 1979). Ulanowicz' concept of ascendancy can also be seen as a final cause in ecosystem development, although Ulanowicz duly notes that a dialectical relationship exists between ascendancy and a system's overhead or reserve—essentially the capacity of a system to flexibly deal with disturbance (Ulanowicz, 2004; Ulanowicz et al., submitted for publication).

An immature system is characterized by few hierarchical levels; fast processes dominate, e.g., pioneer species with r-strategy lifecycles (Holling, 1992). As a system becomes moderately mature, it is able to capture more energy and throughflow increases, providing a basis for physical structure of greater complexity and information content (Jørgensen et al., 2000). Interpolation of hierarchical level is a common occurrence during intermediate stages of development. As a system matures and is drawn toward the attractor of more efficient entropy production, it becomes more highly structured with a greater number of hierarchical levels (Salthe, 2004a). This may be considered as qualitative change from growth-to-throughflow (Jørgensen et al., 2000). Ultimately, there will be little room for new levels that exhibit process rates differing by at least an order of magnitude from existing levels. Thus the loose vertical coupling that imparts stability to hierarchical systems could be compromised. The system can then be said to be overconnected and exhibits decreasing resilience to disturbance (Holling, 1992). Eventually the system becomes senescent – involving a declining system mass specific energy flow – and the complex dissipative struc-

ture of a mature system is impared. We can see that in the case of Fig. 3 ecological boundaries might contribute to the overconnectedness of a mature system and thus play a role in the degradation of hierarchical structure. This is counterintuitive given the general acceptance of ecological boundaries as functional landscape elements that generally serve to mediate fluxes of energy, information and materials, thereby promoting stability in large-scale systems (Cadenasso et al., 2003a).

The "pull" of the Second Law of thermodynamics also underlies Salthe's work on the interpolation of new hierarchical levels in a system (Salthe, 2004a). The conditions for the emergence of new levels are as follows: (1) the entropy production of the higher (+1) level increases, (2) the dynamic at the newly created focal level does not create mutual interference with existing dynamics at other levels (i.e., at least an order of magnitude of difference must separate each level's characteristic process rates), (3) boundary conditions must include energy gradients capable of sustaining this new structure, (4) initiating conditions must be present (Salthe, 2004a). In the case that the new level represents an ecological boundary, the supersystem could be considered to be a larger landscape mosaic of ecosystems (e.g., System A in Fig. 2B). The emergence of new subsystems on any given (pre-existing) hierarchical level would also be in line with the Second Law given such emergence creates greater overall entropy production in the supersystem. A new subsystem within a pre-existing level by definition would not achieve dynamical separation with adjacent subsystems (Salthe, 2004a). Thus, the only way that entropy production could be enhanced at higher levels would be through the dynamical rate separation of adjacent systems. This insight might explain the tendency of ecological boundaries to be active in the processing and transmission of signals coming from either side: if such processes provide needed materials, information, or energy to the adjacent ecosystems and thereby facilitate growth and diversity, then this role of ecological boundaries would be favored thermodynamically. Furthermore, if an ecological boundary increases energy throughput compared to at least one of its adjacent systems then it might be favored as well.

The nature of the fluctuating conditions at ecological boundaries often precludes a boundary system developing much past an intermediate stage (not to mention that if both adjacent systems are approaching climax, then a boundary would cease to exist) (Forman, 1995). Thus, we propose that ecological boundaries might be expected to have high intrinsic energy flows, a property of immature to intermediate systems. Given a certain amount of system biomass, high specific energy flows (throughflow) would be favored thermodynamically. This would explain (1) how ecological boundaries could persist in time even though disturbance is often recurrent, and (2) why ecological boundaries appear to be such highly functioning systems to many observers. A difference should be recognized, however, between boundaries that occur at stable abiotic gradients (referred to by (Peters et al., 2006) as stationary transitions) and boundaries that are associated with biotic or abiotic disturbance regimes, i.e., grazing, fire, flooding (referred to by Peters et al. (2006) as shifting transitions).

5. Conclusion

Discussing a comprehensive framework for the study of ecological boundaries, Cadenasso et al. (2003b) ask how boundaries "defined by contrasts in architecture, composition, and process, are similar or different in structure and function". In light of the foregoing presentation of boundaries in the context of hierarchy theory, investigators might also ask how the position of an ecological boundary in a hierarchical system affects its structure and function. A characterization of the frequency of principal cycles in a boundary and neighboring systems can help an investigator establish their relative hierarchical levels. The conceptual models discussed here would help in the development of hypothesis about the role of a particular boundary in the context of a larger mosaic of hierarchically ordered patches or subsystems. In particular, hierarchy theory provides insight into how signals from different levels can act as constraints, perturbations, initiating conditions, or simply have a negligible effect on the behavior of nearby subsystems.

Boundaries with higher frequency behavior than neighboring systems are often viewed as functionally important elements of the larger landscape (McClain et al., 2003). However, a hierarchical perspective leads us to question the universality of the idea that ecological boundaries are control points or drivers of broader system dynamics (Cadenasso et al., 2003a; Peters et al., 2006). Other conclusions and observations made here: (a) as a system develops, the interpolation of hierarchical levels between neighboring levels can lead to overconnectedness and eventually to the instability of the system in question, (b) components of lower levels are constrained by higher levels, in essence creating a constraint envelope that allows a certain predictability of component behavior, (c) the Second Law of thermodynamics can serve as a final cause for the emergence of new levels in a hierarchy and new subsystems on a given level when entropy production increases in the supersystem, (d) generally, ecological boundaries are systems in immature—intermediate stages of development where intrinsic energy flow is high (Holling, 1992; Salthe, 2004a; O'Neill et al., 1986). We conclude that boundaries can be more completely understood by creating conceptual models that include constraining components at higher hierarchical levels, reference adjacent systems and their characteristic behaviors, and take into account diachronic patterns of ecosystem development.

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