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Toward Conceptual Cohesiveness: a Historical Analysis of the Theory and Utility of Ecological Boundaries and Transition Zones

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ABSTRACT

Ecological transition zones are increasingly recognized as systems that play a critical role in controlling or modifying flows of organisms, materials, and energy across landscapes. Many concepts describing transitional areas have been proposed over the years, such as the prevalent and durable ecotone concept. Confusion among ecologists and land managers about transition zone concepts and the isolation of studies that use only one transition concept can hinder unified progress in understanding these key systems. Currently, a movement toward conceptual synthesis under the umbrella concept of 'ecological boundary' is underway. Here we examine the history and theoretical baggage of the ecotone, riparian zone, and several other concepts. Subsequently, we present a conceptual cluster analysis, which facilitates a better understanding of the similarities and differences between boundary and transition concepts. We emphasize the hierarchical nature of these concepts: higher-level synthetic concepts can be used in the development of theory, whereas lower-level concepts allow more specificity and the formulation of operational definitions. Finally, we look briefly at the utility and future use of boundary and transition zone concepts.

Key words: ecological boundary; transition zone; ecotone; riparian zone; ecological theory; conceptual cluster; transdisciplinarity.

INTRODUCTION

Many of the principal concepts in ecology continue to present epistemological and operational challenges (O'Neill 2001; Jax 2006). The ecological boundary is one such concept. Numerous terms have been used to describe the area of transition or boundary between ecological units since the introduction of the 'ecotone', by Clements (1905). The theoretical baggage of the ecotone concept and the abundance of similar ecological terms have likely led to some confusion (Van der Maarel 1990; Kent and others 1997). In part to avoid conceptual confusion, a series of papers in *BioScience* examined the core features of boundaries in ecology, offered a theoretical framework for the creation of working models, and provided a series of possible boundary attributes to aid in communication (Cadenasso and others 2003a, b; Strayer and others 2003). In this paper, we build on the work of these authors by (1) presenting a historical analysis of several of the most important concepts related to the ecological boundary, (2) analyzing the dissimilarity between boundary and transition concepts through the use of cluster analysis, (3) contrasting the ecological

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boundary with transition zones such as the riparian zone, and (4) synthesizing historical, theoretical, and practical considerations in a graphical hierarchical framework. Ultimately, this synthetic approach leads us to consider boundary and transition-related terms as comprising a conceptual cluster (sensu Jax 2006).

Historical analysis of scientific concepts can provide valuable insight into their theoretical underpinnings, conceptual or operational weaknesses, and possible change in the future. Ecological boundaries have been often viewed from two distinct standpoints: (1) as the result of the perennial problem of delimiting such critical ecological concepts as community and ecosystem and (2) boundaries as ecological units, worthy of focused research (Daubenmire 1968; O'Neill 2001; Cadenasso and others 2003a). Here we examine ecological boundary concepts—particularly the ecotone concept—as constructs that have been placed in different theoretical contexts as different subdisciplines have come to the forefront of ecology.

Two important trends in ecology have been evident in the evolution of the ecological boundary concept: (1) the progression from a primarily descriptive ecology focused on the classification of ecological entities to a dynamic ecology concerned with the interplay between pattern and process, and (2) the shift from a one-dimensional or spatially aggregated definition and study of ecological entities to a three to four-dimensional perspective that explicitly includes the problem of scaling (Junk 1989; Wu and Loucks 1995; Swihart and others 2002). Despite the formulation of predictive theory in many ecological sub-disciplines during the last century, a body of theory that specifically addresses the function and dynamics of the ecotone and other transition zones has been elusive (Holland 1988; Laurance and others 2001; Cadenasso and others 2003a). This, however, is changing as ecological boundaries are recognized to have important functional roles in human-modified landscapes (Cadenasso and Pickett 2000; Harper and others 2005). In this sense, conceptual clarity is seen as a precursor to continued theoretical development and a requisite for ''enlightened'' empirical studies, conservation projects and management plans.

In addition to the ecological boundary, we examine the idea of transition zones in ecology. One could argue that boundary (the edge or limit of something) and transition (change from one type or form to another) can be reconciled in ecology by employing the concept of grain and extent (Wiens 2002; Gosz 1993). However, at any given scale, the use of ''boundary'' or ''transition'' often implies functional differences in the ecological units under consideration (Peters and others 2006). Thus, some clarification on this issue is required. In the following discussion, the riparian zone is used as a familiar example of a transition zone (Naiman and Décamps 1997).

THE ECOLOGICAL BOUNDARY: HISTORY AND THEORY OF CONTRIBUTING CONCEPTS

In recent syntheses, the ecological boundary has been reconstrued as an inclusive term, replacing or encompassing similar concepts such as the ecotone, ecocline, interface, edge, gradient, transition zone and border (Cadenasso and others 2003a). The boundary concept has been used among plant ecologists when describing distinct transitions between communities (Whittaker 1956). It also became an important concept as patch dynamics and landscape ecology came to the forefront in the late 1970s (Pickett and Thompson 1978; Wiens and others 1986). However, the closely related ecotone concept was the prevailing ecological transition concept for a good part of the twentieth century. In the following sections, we trace the use and alteration of the boundary and the ecotone concepts by three important ecological subdisciplines: community ecology, landscape ecology, and ecosystem ecology.

Communities

Although first mentioned by Livingston (1903), the ecotone concept was developed by Clements who defined it as a tension zone between two vegetative formations—large-scale vegetation units (Kent and others 1997). Later, Weaver and Clements (1929) referred to the ecotone as a mixed community between two other communities of higher rank. It is unclear whether Clements viewed ecotone as a multi-scalar concept or whether he used different (ambiguous) terminology in his different definitions. In any case, Clements clearly conceived of communities as organism-like entities. In this context, the ecotone was viewed essentially as a one-dimensional demarcation line between different vegetative units (Jeník 1992). The key ecotone criterion was an abrupt change in plant species composition. Although Clements' ecotone concept was primarily focused on plant community limits, he did recognize the importance of underlying physical or geological gradients, indicating that ecotones are especially notable where 'the medium changes, as between a pond and prairie' (Clements 1907).

In general, community ecology at the middle of the twentieth century was a descriptive discipline—focused on classification of vegetative formations (Risser 1995; Swihart and others 2002). In essence, the ecotone provided an interesting feature for anecdotal observation but did not itself merit much experimental research. In a 1968 book on plant communities, Daubenmire writes 'ecotones, or habitats of limited extent, must be avoided when selecting sites to conduct experiments if the results are to be extrapolated'. According to Risser (1995), those ecologists that did actively use the ecotone concept often worked at different spatial scales and addressed different research questions.

The tension between Clements' organismic concept of the plant community and Gleason's individualistic concept has affected the evolution of the ecotone concept (Attrill and Rundle 2002). Those ecologists that subscribed to Gleason's individualistic concept questioned whether plant communities were indeed distinct entities identifiable on a landscape. The ecotone—defined as an abrupt transition between community types—became useless as an organizing concept. Instead, the environmental gradients along which plant species aligned became worthy of study (Whittaker 1956; Wilson and others 2004).

A further twist is the existence of a similar term: the ecocline. The ecocline was originally introduced by Clements (1936) and associated with large-scale community change with varying slope and exposure in mountainous areas (Jeník 1992). The ecocline concept was infrequently used until adopted by Whittaker (who rejected the ecotone as ''scarcely understood by ecologists'') to refer to areas of gradual change between communities arising from a gradient in at least one major environmental factor (Whittaker 1960; Attrill and Rundle 2002). As compared to the ecotone, the ecocline has been thought of as more internally heterogeneous and ''environmentally stable'' (van der Maarel 1990). In spite of Whittaker's widespread influence, the ecocline concept was not widely adopted among ecologists outside of plant ecology (Kent and others 1997; Atrill and Rundle 2002).

Landscapes

Landscape ecology examines the mechanisms and consequences of the heterogeneous distribution of organisms, materials and energy across space. In this context, boundaries can play a fundamentally important role as zones of interaction or control points, influencing ecological flows (Cadenasso and others 1997, 2003a; Cadenasso and Pickett 2000; Puth and Wilson 2001). The dominant conceptual model in landscape ecology has been the patch-mosaic model, where patches are envisioned as discrete landscape elements, and borders are distinct linear features rather than continuous transition zones (Forman 1995; McGarigal and Cushman 2005). Several boundary-related concepts are regularly employed in landscape ecology: edge, border, boundary, and corridor (Figure 1). Below, we discuss three ways that ecotones might be defined in terms of landscape ecology terminology.

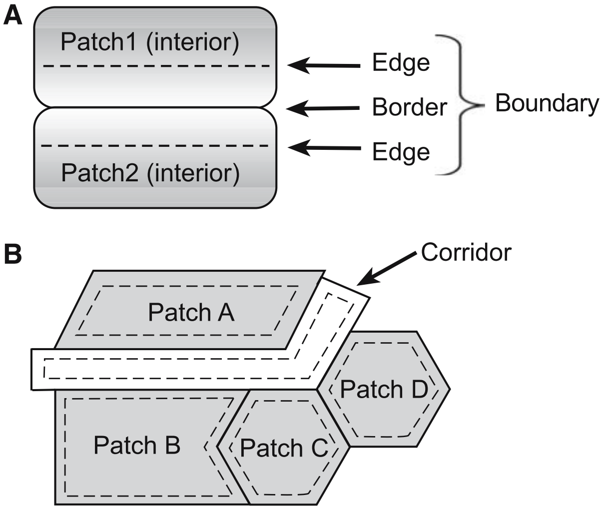

Figure 1. **A** Terms used in Forman (1995). **B** The boundary between two patches (for example, *D* and *C*) closely resembles the ecotone concept; alternatively the corridor might be considered an ecotone from a systemic point of view.

First, given that landscape patches are often based on floristic or physiognomic criteria, a patch border might be thought of as the equivalent of an abrupt transition zone or ecotone. This would be appropriate when the spatial resolution of a study is relatively coarse and/or when the abruptness of the ecotone is such that it is essentially linear with little or no internal function. Although the term 'border' does not conceptually allow for a transitional area between two patches, the idea of such a discrete, linear interface between two vegetation communities does approximate Clements' original concept (Table 1). However, it should be noted that discrete borders presenting a high degree of contrast are often created and maintained by human activities, not the 'super-organismic' community properties described by Clements (Murcia 1995).

Table 1. Definitions of the Ecological Boundary and Related Concepts

Ecotone

Clements (1907): Stress line that connects the points of accumulated or abrupt change... usually well marked between formations, especially where the medium changes, as between a pond and a prairie

Odum (1971): A transition between two or more diverse communities... It is a junction zone or tension belt, which may have considerable linear extent but is narrower than the adjoining communities

Holland (1988): Zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems

Van der Maarel (1990): An environmentally stochastic stress zone

Ecocline

Whittaker (1975): The union of a complex-gradient (assemblage of environmental factors) and the community gradient (represented in terms of populations) to form a gradient of ecosystems or an ecocline

Van der Maarel (1990): A gradient zone, which is relatively heterogeneous but environmentally more stable (than an ecotone)

Edge

Forman (1995): The portion of an ecosystem near its perimeter, where influences of the surroundings prevent development of interior environmental conditions.

Ries and others (2004): Generally defined as boundaries between distinct patch types, the identification of edges depends on how patches are defined within a landscape. Patch definition can occur at a variety of scales

Boundary

Forman (1995): A zone composed of the edges of adjacent ecosystems

Cadenasso and others (2003a, 2003b): Ecological boundaries have three defining features: (1) three-dimensional zones of transition between contrasting systems, (2) the gradient in the feature setting up the contrast is steeper in the boundary than in adjoining systems, (3) boundaries can be wide or narrow, reflecting steepness of the gradient

Interface

Naiman and Decamps (1997): Interfaces between adjacent ecological systems have a set of characteristics uniquely defined by space and time scales and by the strength of interactions between the adjacent systems... interfaces posses specific physical and chemical attributes, biotic properties, and energy and material flow processes

Biotic transition

Peters and others (2006): The boundary and the neighboring areas. Consists of a hierarchy of patches with different properties, spatial arrangements, and connectivity with other patches that determine the response of the transition zone to a range of environmental conditions

The boundary is often defined as being a two or three dimensional landscape element that includes the linear border and the adjacent patch edges (Table 1). Depending on the scale of analysis, a boundary might be considered an ecotone or even an ecocline (Kent 1997). For example, the work of Attrill and Rundle (2002) posited this question (ecotone or ecocline?) for a 110 km segment of the Thames Estuary. They concluded that at this large scale a composite system of two ecoclines (sea to mid-estuary and river to mid-estuary) best described a pattern where intermediate salinity corresponded to the harshest habitat. The ecotone concept—based on the idea of a narrow and relatively homogeneous transition zone—might be applied to transitions between communities or landscape elements within a larger transition zone: the ecocline (van der Maarel 1990).

A voluminous literature has been generated around the concept of ‘edge effect‘ (Gates and Gysel 1978; Murcia 1995; Ries 2004). By definition, it takes two patch edges to form a boundary. However, studies of edges often examine one edge at a time; a typical example is a forest edge studied without explicit consideration of the adjacent edge habitat—often pasture (Murcia 1995). This is conceptually equivalent to studying one half of a transition zone or ecotone. Most edge effects have been studied and observed at a limited range of spatial scales: between 10 and 150 m from a border (Forman 1995; Murcia 1995; Meiners and others 2002; but see landscape studies of insects such as Dauber and Walters 2004). Due to the relative abruptness of the edge transition in these edge effect studies, they are conceptually more in line with the ecotone than the ecocline (van der Maarel 1990;

Forman 1995). Other studies have examined processes along the forest-field ‘edge gradient’ which includes areas on both sides of the border (Willson and Crome 1989; Cadenasso and Pickett 2000; Meiners and others 2002). These studies have provided a more complete picture of the dynamics of the entire boundary area, not just one edge.

In landscape ecology, a corridor is a linear or curvilinear patch that, according to Forman (1995), possesses certain functional attributes such as: habitat, filter, barrier, conduit, source, or sink. Figure 1 shows a situation in which the corridor has edges and interior areas—which are theoretically isolated from the influence of the neighboring patches. As the term ‘corridor’ implies, a major focus in landscape ecology is the study of longitudinal movement of organisms or materials through corridors and the impact of corridors on landscape connectivity (Goodwin 2003). If viewed perpendicular to its length, a corridor with interior creates a complex transition zone between two wider patches. In this sense, a corridor provides a good approximation of a systemic ecotone, where the corridor or ecotone interior exhibits emergent behavior. Puth and Wilson (2001) point out that boundaries and corridors are often considered by researchers and managers to be features that exist independently in nature when, in fact, they are conceptual units based on permeability to specific ecological flows. Thus, a corridor for small mammals may be an impermeable boundary for the flux of detrital material.

The study of the spatial dynamics of ecological phenomena has brought the themes of scale and hierarchy theory to the forefront of landscape ecology (O’Neill and others 1989; Levin 1992). Working with ecotones at the biome-level, Gosz (1993) was the first to describe the ecotone as a nested hierarchy. In hierarchy theory, one identifies ecological entities or interactions of interest, establishes their temporal or spatial scale (based on process rates), and then identifies the lower-level components that make up the entity of interest and the larger system of which the entity is a component. An entity on a particular level will have its behavior constrained primarily by higher-level systems, although limitations from lower-level components can also constrain dynamics at the focal level (O’Neill and others 1989). Using these ideas, Gosz (1993) identified different sets of constraints that might act upon ecotones at different levels in a hierarchy. An ecotone at one level would interact with neighboring patches having similar process rates; the consequences of such interaction might be observed in a higher-level ecotone. One insight gained from this perspective is that different scales of ecotone analysis might identify different functions or patterns if a scale break is crossed and entities on a different organizational level become dominant. Alternatively, the ecotone may be quite similar in pattern or function across scales, indicating fractal behavior and the applicability of power-laws (Halley and others 2004). Finally, a hierarchical perspective of the ecotone can account for the differences between the ecotone and ecocline as laid out by van der Maarel (1990). The ecocline becomes an ecotone occurring at a higher level in the hierarchy and thus having slower, more stable dynamics as described by van der Maarel (1990).

Ecosystems

Several divergent theoretical and methodological pathways are evident within ecosystem ecology (McIntosh 1985). However, three commonalities are relevant here. First, ecosystems are often studied as discrete ecological entities without explicit consideration of transitions between adjacent systems until at least the late 1970s; to this day ecosystem theory has rarely been applied to transitional zones or systems (Risser 1995; Laurence and others 2001). Second, ecosystem ecology has had much success in conceptually simplifying or distilling complex systems by focusing on fluxes of materials and energy. This emphasis on the functional roles of both biotic and abiotic entities within ecosystems is appropriate for the study of transitional zones as functional landscape elements. Third, ecosystems theory is helpful in understanding the emergent behavior of transitional areas (beyond the simple averaging of the behavior of the two adjacent systems).

According to Risser (1995), as ecologists began to study ecosystems spatially in the context of landscapes in the 1970s, transition zones began to be seen as functional elements. Perhaps this shift—perceiving ecosystems rather than vegetative communities as landscape elements—ultimately led to an ecotone definition specifically referring to a ‘zone of transition between adjacent ecological systems’ (Holland and others 1988). Although this shift in language might seem trivial, it effectively placed the ecotone concept in a new theoretical realm. Holland and others (1988) indicate that although the ecotone shares many attributes of the ecosystem or biome concepts, it is unique in its functional role as processor of material flows between ecosystems. Although the ecotone shares many attributes of the ecosystem or biome concepts. Holland and colleagues (1988) further emphasize the importance of ecotones in land management and restoration.

Ecological boundaries have been recognized as having biotic composition, ecosystem functions, and temporal dynamics that are distinct from adjacent systems (Cadenasso and others 2003b). It seems reasonable, then, to view boundaries as ecological systems that are open to fluxes from adjacent systems and exhibit the emergent property of controlling these fluxes. Various authors have discussed how ecotones or transition zones can absorb, amplify, reflect, deflect or channel, and transform flows of organisms, materials or energy from adjacent systems (Kolasa and Zalewski 1995; Risser 1995; Stayer and others 2003; Peters and others 2006). In fact, Peters and others (2006) consider that the dynamics of boundary systems are 'key drivers of landscape change'.

Several authors have suggested that ecotones are highly dynamic and often unstable (stressed) environments (van der Maarel 1990; Attrill and Rundle 2002). If we accept the proposition that ecological systems are drawn toward one or more states or attractors given a certain set of constraints (for example, climatic, edaphic, and biotic potential of species present), then we might expect the boundaries between ecosystems to be quite dynamic indeed. These transitional areas might not only be far from any local steady-states, but they could also be exposed to relatively dynamic 'constraint envelopes' (O'Neill and others 1989; Kay 2000). Citing the work of O'Neill and others, (1989) Fagan and others (2003) point out that the metastability of ecosystems in the landscape (a condition where locally steady dynamics can rapidly change as constraint envelopes vary and critical thresholds are crossed) has important consequences for ecological boundaries. At 'metastable' boundaries, the underlying environmental gradients do not reveal steep rates of change, whereas response variables, close to critical thresholds, change rapidly. Climate change may influence constraint envelopes, creating significant spatial movement of ecological boundaries (Chen 2002). A systemic perspective thus provides some insight into boundary dynamics, a historically under-examined topic.

THE RIPARIAN ZONE AS AN EXAMPLE OF A SYSTEM-SPECIFIC TRANSITION ZONE

The concept of transition zones is not particular to ecology. It is often used in the earth sciences to refer to global phenomena such as the Earth's mantle to core transition zone, or smaller-scale lithological transition zones (Lin and Wang 2005; Fischer and others 2006). The gradient between urban and rural areas has also been viewed as a transition zone with certain emergent characteristics (McDonnell and others 1997; Tang and Chung 2002). In hydrology, the hyporheic zone is a transitional area between stream water and groundwater (Boulton and others 1998). Coastal ecosystems have been referred to as 'critical transition zones' between terrestrial and oceanic realms that play important roles in controlling ecological flows (Ewel and others 2001). Some common characteristics of these transition zone concepts are (1) they refer to specific systems that bound the transitional area, (2) they explicitly have volume and often internal heterogeneity (as opposed to linear borders), (3) they often occupy a limited range of spatial scales determined in a large degree by the identity of the bordering systems, (4) they exhibit behavior or have functional roles distinct from the bounding systems, (5) transitional areas on the Earth's surface at human scales tend to be highly interdisciplinary units of study (for example, riparian zones, urban-rural transitions, coastal zones).

The riparian zone occurs in a specific landscape context: the area between aquatic and terrestrial systems, which is regularly influenced by fresh water (Naiman and others 2005). The contrast between terrestrial and aquatic systems underlies the functional importance and often, dynamic behavior of riparian transition zones. Fluvial systems, characterized by multiple (and multi-dimensional) physical, chemical, and biological gradients also tend to be dynamic. Such fluvial dynamics are one of the principal drivers of riparian pattern and process, although simultaneously the riparian zone modifies and constrains the fluvial system (Gregory and others 1991). Riparian zones can act as filters or control points by processing the flows of energy and materials from terrestrial environments that cross their upper topological limit (Naiman and Décamps 1997). Clearly the study of riparian zones is interdisciplinary, requiring understanding of hydrological, geomorphic, biochemical, and socio-economic forces (Groffman and others 2004; Naiman and others 2005; Thorp and others 2006).

The common use of the riparian zone concept in the scientific literature began approximately 30 years ago (NRC 2002). It is likely that the concept's rapid acceptance had to do with its synthetic power—integrating useful knowledge and methodologies from several scientific fields. Additionally, the buffer functionality of riparian systems was understood early on (Karr and Schlosser

1978). Thus, the concept was incorporated in environmental regulations as well as conservation and restoration plans. In the following passages, we examine the theoretical context of the riparian zone and its utility for ecological investigation. Unlike the ecotone concept, the riparian zone did not arise in the context of community ecology; however it does share important links with landscape ecology and ecosystem science.

Landscapes

Several aspects of landscape ecology are relevant and useful in the study of riparian zones. First, the idea that the relative position of ecological entities or processes in the landscape can be important in their behavior through time is central to landscape ecology (Wiens 2002). This is clearly the case in riparian zones where small distances from the fluvial channel can influence species composition, community succession, biogeochemical processes, and the impact of human activity. Second, various authors have commented on the hierarchical nature of riparian corridors, where processes operate from a temporal scale of seconds to thousands of year (Gregory and others 1991; Poole 2002). A landscape ecology approach—especially a hierarchical patch dynamics approach—allows for the study of patterns and processes on multiple scales (Wu and Loucks 1995; Poole 2002). Although conceptual models of fluvial systems have historically emphasized the continuous nature of rivers and their riparia, it appears that considering river corridors as patchy and discontinuous is a more accurate mental model and lends itself to landscape ecology techniques developed for terrestrial systems (Vannote and others 1980; Wiens 2002; Thorp and others 2006). Finally, landscape ecology facilitates the integrated study of watersheds and the inclusion of human communities in the study systems (Naiman and others 2005).

As with the case of the ecotone, the riparian zone concept has been visualized in different ways, generally with an increase in its dimensionality over time. The most notable spatial dimension of the riparian zone is its length (parallel to flow in the adjacent fluvial system). Forman (1995) defines riparian corridors as the floodplain portion of the river corridor. 'The river corridor,' writes Forman, 'should be thought of as a giant tube in dynamic equilibrium.' Ward (1989) proposed a four-dimensional concept of fluvial systems, drawing attention to dynamics occurring in other dimensions such as interaction between the fluvial and riparian systems. The lateral dimension had often been overlooked in human impacted rivers where dredging, dike construction and channel simplification have reduced the complexity of floodplains and other riparian areas (Ward 1989; Naiman and others 2005). A vertical dimension refers mainly to the hyporheic zone, which some authors refer to as an ecotone between groundwater and surfacewater (Boulton and others 1998). The role of hyporheic flowpaths as sources or sinks of nutrients in structurally complex riparian zones is underscored by Naiman and others (2005). It is also relevant that Ward mentioned the temporal dimension because dynamic and stochastic hydrological patterns (especially in less altered systems) drive patterns of temporal patches in the riparian/riverine landscape (Thorp and others 2006).

Ecosystems

Like the ecotone, the riparian zone is frequently defined as a transition zone between ecosystems, and occasionally an ecosystem or mosaic of ecosystems in its own right (Gregory and others 1991; Fisher and others 1998). In this sense, ecosystem theory can be appropriately applied to riparian zones although, as Fisher and others (2001) point out, river ecologists have recently looked more to landscape ecology for conceptual models and tools.

Expanding on the nutrient spiral concept, Fisher and others (1998) proposed a 'telescoping ecosystem model' for examining material retention in lotic systems. The model includes riparian and hyporheic zones as subsystems contributing to nutrient and material cycling in rivers. The model indicates how the riparian zone can play a role in controlling biogeochemical and physical properties of the fluvial system. As the outer concentric cylinder of the model, the riparian zone is predicted to have a higher resistance but a lower resilience to flood events in terms of material processing than the surface stream. Furthermore, the model emphasizes that the linkages between the subsystems, hypothesizing that inter-subsystem flows would increase the resilience of the system as a whole. Although Fisher and colleagues (1998) discuss ways this model could be expanded to include lateral exchange with terrestrial systems or spatial patchiness, the model has had limited use elsewhere.

The hierarchical patch dynamics model (Wu and Loucks 1995), later adapted for riverine corridors (Poole 2002), is considered a useful conceptual model by the authors of a recent synthesis of riverine theory (Thorp and others 2006). Wu and Loucks (1995) draw in concepts from ecosystem theory and landscape ecology, fundamentally hierarchy theory and the principle that spatial patchiness is ubiquitous in ecological systems. At each hierarchical level, a particular study system is composed of a mosaic of interacting patches that are characterized by similar process rates or breaks in certain spatial or organization patterns. These authors also used many strands of ecosystem theory such as non-equilibrium thermodynamics, the theory of dissipative structure and the properties of non-linear systems (domains of attraction and state changes). Hierarchical patch dynamics includes the principle of incorporation—whereby non-equilibrium patch processes are incorporated into the dynamics of higher levels and effectively smoothed out (Wu and Loucks 1995). This conceptual framework indicates that riparian zones are likely to have dynamic, non-linear behavior, but that certain properties will emerge from interactions between biotic and abiotic components (Naiman and others 2005). Incorporation is a helpful way to think about how disturbance regimes imposed by adjacent systems can, to some degree, be modulated by riparian zones. The hierarchical patch dynamics perspective also facilitates linkages between conceptual models of fluvial systems, riparian transition zones, and terrestrial systems (Poole 2002).

Gregory and colleagues (1991) base their analysis of riparian zones on fluvial geomorphology, which essentially provides a physical template for riparian ecosystems. In this view, the distribution and composition of riparian vegetation reflects the external disturbance regimes of floods and landslides. This idea was systematized by Montgomery (1999) as the process domain concept, where hill slopes, fluvial channels, and floodplains each have different disturbance regimes and play distinct roles in the transportation of sediment. Gregory and others (1991) describe how the retention of organic material and sediments in fluvial systems creates a functional connection between geomorphic and fluvial processes, on one hand, and riparian vegetation and aquatic biota, on the other. Areas of the riparian zone disturbed by flood events or landslides become patches at different hierarchical levels in a mosaic of self-organizing ecological systems.

To sum up, a historical analysis can point out differences in usage or theoretical context of similar concepts that can ultimately cause confusion and delay synthesis. For example, the ecotone concept arose as an abrupt transition between communities or ‘complex organisms‘ in Clements‘ language (1936). By the late 1980s the ecotone had been adapted for use in ecosystem ecology and landscape ecology and had been imbued with a series of functional and structural characteristics that have often been hard to demonstrate in the field (Holland and others 1988; Walker and others 2003). The ecotone and similar concepts were ultimately subsumed within the ecological boundary by Cadenasso and others (2003a), however, these other concepts continue to be used independently of the ecological boundary concept and it appears that further conceptual clarity is needed. The riparian zone is often seen as a more concrete concept due to its fixed landscape context. Nevertheless, as a conceptual unit it has evolved considerably, from a primarily longitudinal focus associated with the river continuum concept to a four-dimensional system with numerous functional characteristics (Vannote and others 1980; Ward 1989; Naiman and others 2005).

SYNTHESIS

The use of theoretical constructs in ecology is indispensable in the comprehension of complex systems and interactions. Often, researchers use concepts without making explicit which of the various definitions of the term they are using or justifying the use of a particular concept over similar ones. It is unlikely that those who regularly use boundary or transition concepts would agree on specific definitions or the reduction in the number of related concepts. This is why we find it important to (1) attempt to visualize the difference (and similarities) between some of the most common existing terms, and (2) emphasize the hierarchical nature of conceptual definitions.

Classifying Boundary and Transition Concepts

In the following passage we list some criteria that are potentially useful in clarifying conceptual dis(similarity). These criteria can aid in the formation or clarification of the generic meaning associated with each concept, although actual application of the concepts to study systems will likely require the creation of more specific operational definitions (Jax 2006). These criteria are then used to group a series of boundary and transition concepts. For dichotomous criteria, two levels are assigned; for other criteria we have used a three level nominal scale. For each criterion, values were assigned to each boundary or transition concept according to our reading of the relevant literature and shown in Table 2.

Degree of Internal Resolution at Scale of Interest. This criterion is best thought of as a continuum between low resolution (where the longitudinal

Table 2. Matrix of Values ascribed to Boundary and Transition Concepts

Criterion	Ecological boundary (Cadenasso and others (2003a, b; Fagan and others 2003)	Edge (Murcia 1995)	Riparian zone (Naiman and Decamps 1997)	Ecotone 1 (Clements 1907)	Ecotone 2 (Van der Maarel 1990)	Ecotone 3 (Holland and others 1988)	Ecocline (Whitaker 1960)	Corridor (Forman 1995)	Biotic transition (Peters 2006)	Critical transition zone (Ewel and others 2001; Levin and others 2001)
Internal resolution	2	1	3	1	1	2	3	2	3	3
Scale-applicability	3	2	1	2	2	2	1	2	3	2
Interdisciplinarity	2	2	3	1	1	2	1	2	2	3
System-specificity	3	2	1	2	2	3	2	3	2	2
Boundary definition	2	2	3	1	1	2	1	2	2	3
Boundary delineation	2	1	1	1	1	2	1	1	1	2
Ontological status	2	2	2	1	2	2	2	2	2	2
Referential dynamics	2	1	2	1	2	3	1	1	2	3

The meaning and valuation of the different criteria are discussed in the text.

dimension becomes dominant and few if any internal components are visible) and high internal resolution (where the area or system of interest is quite internally heterogeneous). Assignation of values: (1) low resolution; (2) medium resolution; (3) high resolution.

Scale-Applicability. The different concepts considered here have often been described and used at particular spatial scales. Although theoretically, many concepts could be used at any scale (Cadenasso and others 2003a), here we use the scale implied by the defining author or the most common scales at which the concept has been applied. Assignation of values: (1) specific scale of applicability; (2) limited range of scales; (3) fully multiscalar.

Degree of Interdisciplinarity. This criterion is undoubtedly subjective. However, we felt it was important to take into consideration the degree to which workers using different concepts were able to integrate their conceptual models, research methods, and finally understanding of the salient questions. We base our classification mainly on the cited publication associated with each concept, but also on the historical analysis presented above. Assignation of values: (1) limited to one or two ecological subdisciplines; (2) limited primarily to ecology and environmental science; (3) fully interdisciplinary, explicitly considers social, economic, and physical themes.

System-Specificity. Some concepts have been envisioned as the transition or boundary between certain ecological systems. Others, like the ecological boundary, are explicitly system-independent (Cadenasso and others 2003a, b). Assignation of values: (1) system-specific; (2) limited to certain classes of systems; (3) system independent.

Boundary Definition: Structural or Functional. Boundaries are often thought of as having both structural and functional characteristics, and thus this criterion is best envisaged as a continuum. Structural boundaries tend to be viewed as static, whereas functional boundaries are often seen as dynamic (Peters and others 2006). Assignation of values: (1) primarily structural; (2) equal emphasis on structural and functional characteristics; (3) primarily functional.

Boundary Delineation: Structural or Functional. This criterion is related to the previous, but refers more specifically to how the concept is delineated—that is, how it is separated from neighboring or similar systems (Jax and others 1998). The use of structural boundaries is often more workable when a boundary concept is translated into an operation definition (Fagan and

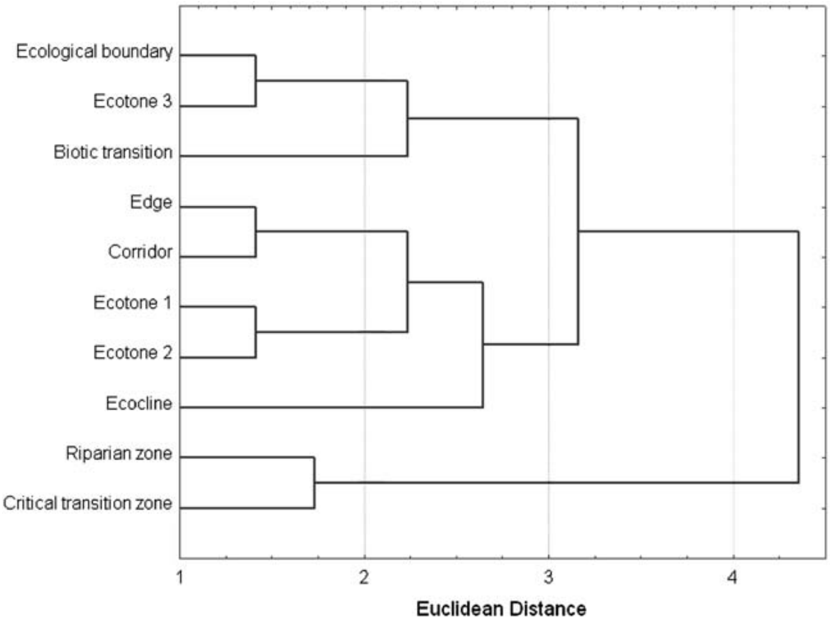

Figure 2. Results of conceptual cluster analysis. The tree diagram was generated using the complete linkage algorithm.

others 2003; Jax 2006). For this reason, many concepts that are defined as functional units are then delineated using structural criteria. This can lead to the problematic issue of inferring process from pattern (Jax 2006). Assignation of values: (1) primarily structural delineation; (2) both structural and functional delineation possible; (3) primarily functional delineation.

Ontological Status. This is an important, but often not explicit, aspect of ecological concepts. How one views the concept they are studying in an abstract sense often influences later practical decisions. Jax (2006) refers to the idea that the ecological concept in question exists as such in nature as an ontological perspective, whereas an epistemological or constructivist approach understands that ecological concepts are constructs that do not exist independent of an observer. Assignation of values: (1) ontological approach; (2) epistemological approach.

Referential Dynamics. This term is adopted from Grimm and others (1992) and refers to whether the dynamics of a given system are viewed as (1) steady-state (little observable change on a human time scale), (2) dynamic and predictable, (3) dynamic, occasionally presenting sudden regime shifts, or (4) essentially unpredictable (chaotic).

The matrix shown in Table 2 was used in a hierarchical cluster analysis in Statistica version 6.0. We used the complete linkage joining algorithm and Euclidean distance to produce compact clusters. The results of the cluster analysis are represented in Figure 2. One notable aspect of Figure 2 is that the riparian zone and the critical transition zone form a distinct cluster. Within the second large cluster several concepts appear as quite similar: the edge and corridor concepts, the ecotone 1 and 2, and the ecological boundary and systemic ecotone (ecotone 3). There appears to be a differentiation in Figure 2 between concepts that incorporate more recent theoretical trends in ecology (attention to scale and hierarchical properties of landscapes and the dynamic interaction between pattern and process) and older and more structural concepts.

Conceptual Clusters: A Graphical Hierarchical Model

We propose that ecological boundaries and transitions zones make up a conceptual cluster. According to Jax (2006), a conceptual cluster is a group of concepts that share similar epistemological characteristics, meaning and function in ecology, and phenomena or emergent properties. The utility in making this cluster explicit is that researchers working at different scales and in different systems can begin to draw parallels and share theoretical developments. It also can help clarify the concepts it contains, perhaps allowing redundant concepts to be merged or discarded. Furthermore, the idea of a conceptual cluster works well in a hierarchical framework for dealing with important ecological concepts. Empirical work and applied modelling require that we move toward operational definitions or operational models of more theoretical concepts. On the other hand, theory is advanced by

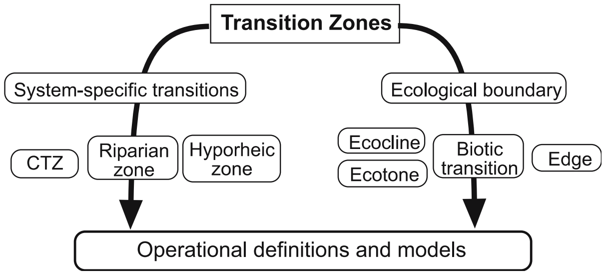

Figure 3. Hierarchical conceptual model of the relation between transition and boundary concepts. The vertical dimension represents a continuum from general/theoretical concepts at the apex, to specific/operational definitions of these concepts at the base. CTZ stands for Critical Transition Zone.

moving in the opposite direction, toward higher levels in the conceptual hierarchy, and by looking for parallels in transitions between other systems or within other disciplines (Cadenasso and others 2003b). In Figure 3, a conceptual hierarchical framework is shown. Here we make a distinction between system-specific transitions and concepts closely related to the ecological boundary. Each of the lower-level concepts can be considered a transition zone and exhibits a propensity toward certain functional characteristics (Popper 1990). Furthermore, the conceptual cluster imposes restrictions on the nature of the nested concepts (Wu and David 2002).

Operational Definitions

General definitions that attempt to establish the generic meaning associated with ecological concepts are often broad enough to avoid certain epistemological traps. However, as researchers move from a general definition to an operational definition that specifies more precisely the boundary phenomena of interest and the criteria to be used in delineations, several common problems arise. Frequently researchers see a certain concept, such as they have defined it, as taking on an independent and objective existence. This is the error of reification (Palmer and White 1994), and it can be a problem even if an epistemological approach is taken toward the general definition (Jax 2006). Thus, it is important to clarify from the outset what ecological flows are being examined and to establish spatiotemporal bounds of the question being asked (Cadenasso and others 2003b).

It is crucial for researchers to clarify the difference between ecological boundaries or transitions that are (1) based on the conceptual or empirical delineation of the surrounding systems and (2) located through an independent determination of their boundaries. There are difficulties with both of these approaches to delineation. If an operational definition is based on (1) and it is acknowledged that ecological systems are theoretical constructs with limits that are arbitrary established in space and time, then one arrives at the conclusion that the ecotone is located arbitrarily in space and time (Kolasa and Zalewski 1995). An attempt can be made to reify the bounding ecosystems so that their limits are more concrete in the 'real world'. This leads to another problem: the ecosystem becomes empirically slippery and ultimately unfeasible as an object of study. If bounding systems are to be used in operational definitions of ecological boundaries, they probably should be based (and delineated) on the same questions or phenomena as the boundaries themselves.

The independent delineation of the boundary system is probably preferred, although not entirely free of problems. Many edge detection methods (such as spatial clustering) identify the places of greatest change in some variable of interest and might be useful in locating the center of a boundary system (Fagan and others 2003). However, this still leaves the problem of defining the boundaries of the system. Furthermore, many boundary and transition concepts include functional aspects that are notoriously difficult to repeatedly and unequivocally locate in space. This issue is not easily solved and represents one of the areas of current research in boundary studies (Fagan and others 2003). In general, the ecological relevance of a boundary or transition zone will tend to increase with the spatial overlap of: (1) multiple environmental gradients, (2) ecological and biogeochemical processes that present important quantitative or qualitative changes, (3) marked physiognomic contrast between adjacent systems, and (4) evidence of historical existence.

The creation of operational definitions is not limited to epistemological or scientific considerations but is often tied to political, social, and regulatory concerns, many of which can seem completely arbitrary to the ecological investigator. Nevertheless, it is increasingly recognized that the scientific community has a responsibility to do research that can be used in policy formulation and ecosystem management (Naiman and others 2005). Thus it is vital that scientists familiarize themselves with operational definitions utilized by regulatory agencies so that their research will complement the relevant body of existing work. Furthermore, the scientific community can help ensure the clarity, workability, completeness, and theoretical relevance of operational definitions by actively participating in the often difficult and compromising process of establishing regulatory operational definitions. As an example, every relevant federal agency in the United States has its own definition of ''riparian'' (NRC 2002). In each, the emphasis and level of specificity is slightly different. The operational definition of the US Forest Service (2000), which specifies a horizontal distance of 100-feet from permanent water bodies, clearly shows that compromises are made as one moves vertically from more general concepts to definitions that allow delimitation and regulation. Unfortunately, the work carried out under specific operational definitions is often not subsequently analyzed at higher, more synthetic levels. When such analyses are carried out, they can show that original concepts and theory need to be modified (for example, Zelder and Callaway 1999).

Looking Ahead: Utility of Different Concepts

We see transition zones concepts as an exciting area of investigation in the future because (1) they are often understood as functional and dynamic systems, (2) they are both influenced and influence human use of landscapes, and thus (3) generated knowledge is usually very relevant to management or restoration plans, (4) in many cases a transdisciplinary approach is desirable or required, and (5) there is a need for further theoretical development. Below we discuss the ramifications for the concepts described in previous sections.

The ecotone concept is perhaps the oldest boundary concept in ecology and has changed significantly over its 100-year history. Two factors can help explain this extended period of utility: (1) the successful placement of the concept in different theoretical or conceptual contexts, specifically ecosystem theory and landscape ecology; (2) the intersection between the lack of a general ecological theory of transition zones and the desire of ecologists to describe and study transition zones. However, the ecotone concept is now attached to a significant amount of theoretical baggage from different subdisciplines and historical periods that confuse comparisons between different types of ecotones on different spatial scales. So where does this leave the ecotone concept? Its continued use, especially in the context of landscape ecology (for example, Arnot and others 2004) and plant ecology (for example, Traut 2005) indicate that it is not yet obsolete. However, the ecological boundary represents one of the current pushes toward the unification of significant segments of ecological theory (Allen and Hoekstra 1992; Kay 2000; Cadenasso and others 2003a; Thorp and others 2006). Such efforts at synthesis serve to clarify existing theory, connect scattered but related concepts, and underscore areas requiring urgent work. Because of these advantages, we think that the use of the ecological boundary concept will continue to grow in the ecological literature, whereas the use of ecotone concept will gradually decrease.

Unlike Cadenasso and others (2003a), we think the ecological boundary can be included in yet a more general conceptual level: that of transition zones (Figure 3). Together all these concepts can be considered a conceptual cluster. Thus the ecological boundary and riparian zone share common theoretical underpinnings, but are dissimilar enough to be considered on different branches of the conceptual hierarchy. Although, they are functionally, structurally, and taxonomically diverse, riparian zones and critical transition zones can be grouped as a particular type of system due to the common constraints applied by adjacent systems and a specific position in the landscape. On the other hand, the ecological boundary and related concepts can be applied to many different types of ecological systems —air–land, sediment-water column, and forest-grassland are all valid examples (Cadenasso and others 2003a). Furthermore, the ecological boundary is scale-independent—biome transitions and the boundaries between a root and its soil matrix can be examined with the same conceptual framework (Chen 2002; Belnap and others 2003). The riparian zone can also be studied at different spatial scales, but the range of spatial scales occupied by the transitional areas between terrestrial to aquatic systems is limited. Another difference is that the ecological boundary is defined as overlaying a gradient that is steeper than in adjacent systems, whereas the riparian zone overlays multiple discontinuous gradients and is commonly delineated according to landscape position not rates of change in environmental variables (Cadenasso and others 2003a; Verry and others 2004). A distinction should be made between simple gradients and complex gradients. The first term is implied in the current context where ecotones or boundaries are delineated in reference to simple factors. The later term has been used by Whittaker (1956) to refer to 'moisture' or 'elevation' gradients in which numerous interacting physical factors underlie the gradient in question.

The conceptual cluster of transition zones encourages researchers to compare their specific results to the larger developing theoretical framework (Cadenasso and others 2003a). The hierarchical structure of Figure 3 implies that the lower-level concepts can be more specific, augmenting their usefulness to particular study systems or more practical questions (Jax 2006). Thus we can see that the concept of ecological boundary is useful in providing a framework for the study of transitions between ecological systems, allowing a synthesis of existing ecological theory. The system-specific transition zone, on the other hand, allows one to be more specific about landscape context, spatial scale, and type of dynamics, while opening up the discussion to a wide range of disciplines and allowing the formulation of regulatory operational definitions. We propose that the ecological boundary will find its primary utility within scientific circles, whereas the system-specific transition zone is quite useful in public discourse and socio-economic decision-making.

The work of Nilsson and others (2003), although not precisely about transition zones, does provide an example of the conceptual distinction described here. These authors propose a transdisciplinary approach that focuses on obstacles in communication between disciplines. By recognizing areas of incomplete research in each discipline and the type of data from one discipline required for further advancement in other disciplines, progress on problems relevant to human society will be sped up and the integration of discipline-specific models will be furthered. Nilsson and colleagues discuss this approach as it relates to the problem of land-use impacts on freshwater fluvial systems (system-specific). Focusing on one system (or a small set of systems) at a time facilitates the participation of investigators from different disciplines, NGOs, and governmental agencies.

CONCLUSION

Whittaker (1956) questioned the usefulness of the ecotone and transition concepts in general when he wrote that: "'transition,' 'boundary,' 'tension zone', and 'mixture' represent human attitudes or interpretations imposed on vegetation". However, five decades later, many of these concepts are still actively used by ecologists, although clarity about their meaning and theoretical context is often lacking (van der Maarel 1990). This continued use underlines the utility of such theoretical concepts in the formulation of research questions and the synthesis of research results. Conceptual confusion can spring from the numerous definitions, both general conceptual definitions and specific operational definitions. Confusion can also arise from viewing transitional concepts as existing independently from an observer. We have traced the evolution of several related transition zone concepts—demonstrating that their meaning has changed over time as they have been used in different theoretical contexts. The cluster analysis of similar concepts shows that more recent (or recently revised) concepts tend to group together. The cluster analysis also shows that transition zone concepts that are applicable to specific landscape contexts form a different cluster from concepts that are more closely related to the ecological boundary. By placing the results of this cluster analysis in a conceptual hierarchical diagram (Figure 3) we aim to provide a simple but useful way of incorporating the difference between certain concepts but at the same time illustrating that all concepts can be considered part of a conceptual cluster—that is, a group of concepts that share similar epistemological and function characteristics. Furthermore, a hierarchical view emphasizes the difference between fairly abstract, high-level concepts, and their operational definitions, which allow the translation of ecological constructs to the material world.

As humans create more transitional areas through fragmentation of existing systems and the creation of novel ecological systems, the importance of clarity among transition zone and boundary concepts will only increase (Murcia 1995; Hobbs and others 2006). We see two principal lines of work for the future. First, the creation of operational definitions for specific transition zone concepts for specific systems. Although involving scientists, this work will be carried out in a socio-political context that requires compromise. Second, the creation of conceptual models and the formulation of hypothesis about the dynamics of transition zone concepts. We see an important role for theoreticians in exploring the functions of transition zones and positing hypotheses that could be tried in the field. Ultimately, the hierarchical conceptual model of the transition zone conceptual cluster could help facilitate communication between these lines of work.

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