A Classification of Ecological Boundaries

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Ecologists use the term boundary *to refer to a wide range of real and conceptual structures. Because imprecise terminology may impede the search for general patterns and theories about ecological boundaries, we present a classification of the attributes of ecological boundaries to aid in communication and theory development. Ecological boundaries may differ in their origin and maintenance, their spatial structure, their function, and their temporal dynamics. A classification system based on these attributes should help ecologists determine whether boundaries are truly comparable. This system can be applied when comparing empirical studies, comparing theories, and testing theoretical predictions against empirical results.*

Keywords: boundaries, edges, ecotones, landscape ecology, patches

Studies of boundaries are an important and rapidly evolving part of contemporary ecology (e.g., Fagan et al. 1999, Turner et al. 2001, other articles in this issue of *BioScience*). It is clear from reading the ecological literature that ecologists attach a range of meanings to the term *boundary,* presumably to accommodate the systems and questions they are studying. In view of the rich diversity of kinds of boundaries, both in real landscapes and in conceptual models, it is probably counterproductive to insist that all ecologists agree on a single rigid definition of a boundary. However, if ecologists are to use *boundary* to mean different things on different occasions, it is important to specify the concept of boundary that is being used (Cadenasso et al. 2003). Generalizations and theories about boundaries may apply only to a subset of boundaries with particular attributes, and different study designs may be best suited to different conceptualizations of boundaries. Imprecise terminology will impede the search for general patterns and theories about ecological boundaries.

We have developed a classification of boundary attributes to aid communication and theory development. Our intent is twofold: (1) to expose the wide but sometimes subtle differences among concepts of ecological boundaries currently in use; and (2) to list some of the attributes of boundaries that should be considered when designing a field study, modeling boundaries, or comparing different field studies or models of boundaries to one another.

A classification

Ecological boundaries can be classified in many ways. We have tried to build a classification system that is simple and practical and that includes most of the boundary characteristics that ecologists care about. We consider four main classes of boundary traits: (1) origin and maintenance, (2) spatial structure, (3) function, and (4) temporal dynamics (see box). These characteristics cover the range of boundary attributes

that ecologists have considered. We recognize that many of these attributes are related to one another and may interact in ecological boundaries, but we have artificially isolated them to make the classification clear and complete. We deliberately chose to illustrate this classification with a wide variety of examples to emphasize that concepts about ecological boundaries can be extended beyond the studies of vertebrates and vascular plants that have historically dominated the field.

Origin and maintenance of boundaries. Boundaries can arise in various ways. We first distinguish between what we call investigative boundaries and tangible boundaries. Did the boundary originate in a scientist's mind or in nature? For many ecologists, boundaries are human constructs: lines on a map drawn by a scientist that may or may not correspond with any obvious physical discontinuities in nature. In fact, the arbitrary placement of boundaries for the convenience of a scientific study is a central tool of ecology (Likens 1992, Adler 1998) and other sciences. Political boundaries are often used by ecologists as investigative boundaries. Other ecologists think of boundaries as tangible structures that can be identified in nature. Both investigative and tangible boundaries are widely used by contemporary ecologists, and both are useful. It is necessary, however, to be clear when using the term *boundary* to indicate whether an investigative or a tangible

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Box 1. Attributes of ecological boundaries

How did the boundary originate, and how is it maintained?
- Investigative or tangible
- Causal or consequential
- Contemporary or relict
- Endogenous or exogenous origin
- Endogenous or exogenous controls (maintenance or suppression)

What is the spatial structure of the boundary?
- Grain size
- Extent
- Thickness and dimensionality
- Geometry of adjacency
- Interactive or noninteractive
- Abruptness, steepness
- Patch contrast
- Integrity (perforated versus unbroken)
- Geometric shape and tortuosity
- Number of attributes (single or multiple)
- Offsets or congruencies of multiple attributes

What are the functions of the boundary?
- Transformation
- Transmission
- Absorption
- Amplification
- Reflection
- Neutral

How does the boundary change over time?
- Changes in any structural or functional properties
- Mobility (stationary, directional, oscillating, or random)
- Age and history

boundary is meant. In practice, most boundaries that ecologists study are a mixture of investigative and tangible boundaries, involving the imposition of human order onto some real natural structure (Cadenasso et al. 2003). Rarely do ecologists draw investigative boundaries that are independent of real structure, and practical constraints often force at least some degree of arbitrariness onto boundary definition.

Once we restrict our attention to tangible boundaries, we can ask how the boundary arose. Boundaries may arise because of discontinuities between patches (a consequential boundary, such as a forest–field boundary), or they may cause discontinuities between patches (a causal boundary, such as a fence that encloses a herd of cattle). Existing boundaries may have arisen from forces still in operation (contemporary boundaries) or from forces no longer operating at that site (relict boundaries). For example, the boundary between adjacent wind-driven Langmuir cells (elongate, spinning spirals of water) in a lake or ocean is a contemporary boundary, because the structure lasts only as long as the winds

persist, whereas the boundary between glaciated and unglaciated terrain is a relict boundary. Many boundaries are difficult to classify as contemporary or relict because their structure arose from a mixture of current and past forces.

It may be useful to subdivide boundary origins further, depending on the purpose of the study. For instance, we might distinguish between natural and anthropogenic boundaries, which may have very different spatial structures (Turner et al. 2001) and functions. More generally, we could classify boundaries as having exogenous or endogenous origins, arising, respectively, from processes outside or inside the system of patches and boundaries being studied. Boundaries between new lava flows and older vegetation (Aplet and Vitousek 1994) are of exogenous origin. In contrast, a forest edge maintained by the joint effects of succession and seed predation (Sork 1983) would have endogenous origins, as would grazing halos around coral reefs (Ogden et al. 1973), which depend on the foraging distances of algivorous fish or invertebrates that shelter within the reef. Of course, many boundaries arise as a result of a combination of exogenous and endogenous factors. Ephemeral patches of zooplankton can arise from the interaction between wind-driven Langmuir circulation and the behavior of zooplankton (George and Edwards 1973).

Likewise, exogenous or endogenous forces may tend to maintain or destroy a boundary through time. As an example of exogenous forces that strengthen or weaken boundaries, plankton may be concentrated into patches by ocean gyres or dispersed by winds or currents. A boundary between two vegetation types that is reinforced by the grazing preferences of herbivores (Farnsworth and Anderson 2001) is an example of an endogenously maintained boundary.

Several problems prevent the unambiguous classification of boundaries as exogenous or endogenous. First, *exogenous* and *endogenous* are defined with respect to the study system, and different investigators may define the study system differently; therefore, the same process may be regarded as exogenous by one investigator and endogenous by another. Second, many boundaries originate and are maintained not by exogenous or endogenous forces alone but by an interaction between exogenous and endogenous forces (e.g., zooplankton patches). Finally, control of boundary structure and function may shift between exogenous and endogenous forces over time (as in the case of an exogenous, wind-created forest gap whose boundary is later maintained or destroyed by endogenous biological interactions). Nevertheless, a general distinction between exogenous and endogenous origin and maintenance may be useful for generating hypotheses and comparisons.

Spatial structure. We tried to capture the enormous range in spatial structure of ecological boundaries by recognizing 11 attributes (see box). This list is not exhaustive, nor are the characteristics listed independent of one another, but these 11 attributes do provide a reasonably complete description of the spatial structure of boundaries.

As is the case with many features in landscape ecology (Turner et al. 2001), boundaries may be defined or studied using different grain sizes (figure 1a, 1b, 1c; Fagan et al. 2003). As different grain sizes are used, the same physical structure may appear to be very different or may not appear at all. Many of the boundary attributes that we discuss below, such as length, tortuosity, and sharpness, depend on grain size. Consequently, comparisons of these scale-dependent properties across studies must be made cautiously, as must comparisons of field data (which have a grain size) with models (which may have a different grain size or may be continuous and therefore have an infinitely small grain). At a minimum, scientists must choose their grain size deliberately and specify it in their publications (Cadenasso et al. 2003).

The second scale attribute commonly considered by landscape ecologists is extent (Turner et al. 2001), the absolute physical size of a structure (figure 1d, 1e). Although the term *landscape boundary* may bring to mind a structure hundreds of meters to tens of kilometers long, separating patches of hectares to square kilometers, ecological boundaries range enormously in physical extent. Ecologists have studied small boundaries, such as microbial biofilms, soil crusts, leaf boundary layers, and rhizospheres, whose extent is measured in micrometers to centimeters (Belnap and Lange 2001, Belnap et al. 2003). At the other end of the spectrum, boundaries such as forest edges (Turner et al. 1994), the boundaries of biomes

(Allen and Breshears 1998), and oceanographic fronts may be kilometers thick and hundreds of kilometers long. The extent of a boundary is especially relevant when the boundary interacts with a process that has its own characteristic physical scale (e.g., molecular diffusion, the home range of an animal, the dispersal shadow of a plant).

Boundaries may be construed as having thickness (and therefore having the same dimensionality as the patches they separate) or as being infinitesimally thin (and therefore having one less dimension than the patches) (figure 1f, 1g). That is, when considering two-dimensional patches on a map, are the boundaries thought of as zones between the patches or as infinitesimally thin lines around the patches? It is important for ecologists to think carefully about which boundary dimensionality is more appropriate to their research and to be clear about what boundary dimensionality is being used in their study, as different study designs, models, and theories may be applied to boundaries of different dimensions. To some extent, the choice of boundary dimensionality may be set by the abruptness, grain size, and extent of the boundary, as well as by the mind-set of the investigator, the requirements of experimental design, and mathematical tractability. Both conceptions of boundary dimensionality are widely used in empirical and theoretical studies in ecology.

The detailed geometry of adjacent patches can result in several kinds of boundaries (figure 1h, 1i, 1j, 1k). In the simplest
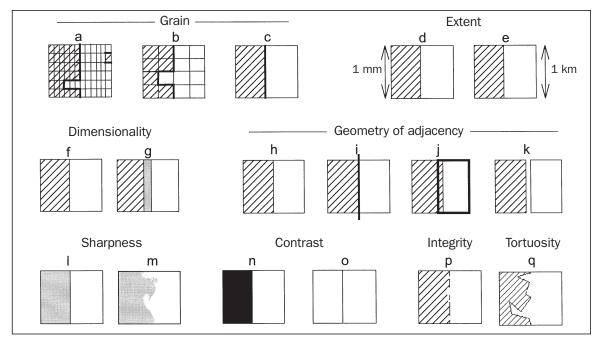

Figure 1. Some attributes of boundary spatial structure. (a) A boundary (heavy line) defined using a fine grain size; (b) the same boundary defined using a medium grain size; (c) the same boundary defined using a coarse grain size; (d) a boundary of small extent; (e) a boundary of large extent; (f) an infinitesimally thin boundary; (g) a boundary with finite thickness (the gray area is the boundary zone, which belongs to neither of the adjacent patches); (h) a boundary between two adjoining patches; (i) a boundary formed by a distinct structure (heavy line) between two patches; (j) a boundary between two overlapping patches; (k) a boundary between two disjunct patches; (l) a sharp boundary; (m) a gradual boundary; (n) a boundary between two highly contrasting patches; (o) a boundary between two slightly contrasting patches; (p) a perforated boundary; and (q) a convoluted boundary.

case, two neighboring patches physically adjoin one another (figure 1h). Adjacent patches may be separated by a third, distinct structure (figure 1i), as when a fence, road, or stream separates patches. Patches may overlap (figure 1j; e.g., home ranges of animals) or not quite meet along the boundary (figure 1k; e.g., a forest and a cornfield separated by a road that is itself not considered to be part of the system under study). The detailed geometry along the boundary between two patches will have important consequences for natural processes and for the design and interpretation of models and field studies.

Conditions in the boundary may be a simple average of conditions in the patches on either side (figure 2a), or they may reflect interactions that occur along the boundary (figures 2b, 2c). We refer to these as interactive and noninteractive boundaries (Lidicker [1999] called them ecotonal and matrix edges, respectively). Many kinds of mechanisms can create interactive boundaries; indeed, much of the literature on the positive and negative effects of boundaries has been focused on identifying, quantifying, and managing these interactions (Phillips 1999, Zheng and Chen 2000, Woodward
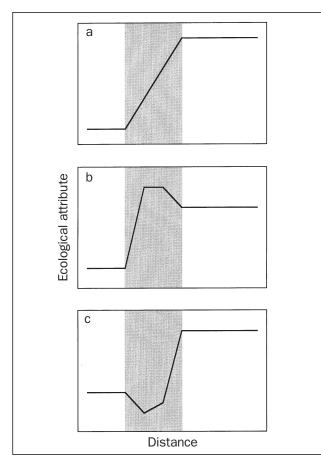

Figure 2. (a) A noninteractive boundary (or matrix boundary, in the sense of Lidicker [1999]); and (b, c) two examples of interactive boundaries (or ecotonal boundaries, in the sense of Duelli et al. [1990] and Lidicker [1999]). The gray area is the boundary, which is conceived as having finite thickness.

et al. 2001). For instance, spillover predation (Holt 1985, Oksanen 1990, Cantrell et al. 2001) of wide-ranging predators sustained in rich patches can intensify prey depression in nearby, unproductive patches. Large populations of Antarctic krill occur just inside the boundary between sea ice and open water, probably because they can find both rich phytoplankton food and refuge from air-breathing predators along this boundary (Brierley et al. 2002). Many biogeochemical reactions (especially redox reactions) take place in boundaries, resulting in the accumulation or depletion of materials in boundaries (Phillips 1999). Boundary interactions may occur regardless of the geometry of adjacency; that is, interactions such as spillover predation do not always require that interacting patches be physically adjacent.

Some people think of boundaries as necessarily being step functions (figure 1l), and some ecological boundaries do fit this model (e.g., the air–water interface or a barbed-wire fence enclosing a grazed pasture). On the other hand, especially if boundaries are thought of as having thickness, the change in ecological conditions across a boundary may be gradual (figure 1m; see also Cadenasso et al. 1997, Bowersox and Brown 2001, Cadenasso et al. 2003, Fagan et al. 2003). The boundary separating a forest from an aging old field and the change from a riffle to a pool in a stream are familiar examples of gradual boundaries. Further, the perception of a boundary as abrupt or gradual will depend on the grain size at which the boundary is being measured or modeled; a boundary that appears abrupt at a coarse grain size may appear gradual at a fine grain size.

The change in ecological conditions across a boundary may be large or small (figure 1n, 1o), depending on the process being studied and the goals of the study. In fact, it is the magnitude of this cross-boundary difference that determines whether the researcher recognizes the existence of the boundary in the first place (Fortin et al. 2000, Fagan et al. 2003). Thus, a specified spatial change in ecological conditions may be perceived as a boundary by one researcher but not by another. Many mechanisms that regulate the exchange of materials, energy, and organisms across boundaries depend on the contrast between neighboring patches, so these contrasts often influence boundary function (Cadenasso et al. 2003). Examples include the gas exchange rate across the air–water interface, which depends on the difference in gas partial pressures between air and water (Cole and Caraco 1998); the movement of animals from one patch to another (Wiens et al. 1985, Holmquist 1998); and the transfer of water and other cloudborne substances, which probably depends on the contrast in vegetational structure across boundaries (Weathers et al. 2000, 2001).

Boundaries may be unbroken (figure 1f) or perforated by conduits (figure 1p). The permeability of a boundary may be determined in large part by the existence and properties (size, spatial arrangement) of such conduits. Thus, Weller and colleagues (1998) suggested that gaps in a riparian buffer would severely reduce the buffer's ability to retain nutrients. Other examples of gaps and conduits through boundaries

include ventilated animal burrows that increase biogeo-chemical transformations across the sediment–water inter-face (Reise 1985) and water lily stems, which are actively ventilated by the plant and which transfer gases across two boundaries (sediment and water and water and air) in lakes (Dacey and Klug 1979). Again, the perception of the integrity of a boundary may depend on the grain size at which it is mea-sured or modeled.

The shape of the boundary, seen from above, may help to determine its properties. Boundaries may be simple (figure 1f) or convoluted (figure 1q). The degree of convolution (tortuosity) may be measured by an index such as the ratio of the actual distance along the boundary to the straight-line distance between the ends of the boundary. As Mandelbrot (1977) noted, however, this ratio may depend strongly on the grain size at which the boundary is being measured. Thus, to compare the tortuosity of different boundaries, the mea-surements must be made at comparable grain sizes or must be subjected to a fractal analysis in which measurements of each boundary are made across a range of grain sizes. Highly convoluted boundaries allow more exchange across bound-aries, whether they are formed by villi in intestines, by com-plex soil crusts (Belnap et al. 2003), or by meanders and anastomosing channels in a river floodplain. Further, the shape of a boundary may determine its temporal dynamics; Hardt and Forman (1989) noted that succession (and there-fore boundary movement and softening) was much faster along concave parts of a forest boundary, where the field protruded into the forest, than along convex parts where the forest protruded into the field.

In the discussion above, we have assumed that bound-aries are defined by a single ecological property (e.g., vegetation type). Many real ecological boundaries are defined by a change in several more or less congruent ecological proper-ties: A forest–field edge, for example, could be defined by veg-etation height, vegetation species, animal species, wind re-sistance, or light penetration. Similarly, many ecological factors covary along vertical gradients in lakes, across shore-lines, or along elevational zones on mountains. Thus, we can distinguish between single and multiple boundaries. Proba-bly few ecological boundaries are purely single in structure.

In cases where multiple ecological properties jointly define a boundary, these properties may be spatially congruent with one another, or they may be offset. Thus, Cadenasso and colleagues (1997) and Cadenasso and Pickett (2000) found that physical factors such as temperature and humidity, as well as herbivore activity, were significantly offset from the posi-tion of a forest–field edge and from one another. Offsets along boundaries may have important ecological conse-quences. For instance, photosynthetically active radiation penetrates farther into desert crusts than ultraviolet radiation; desert algae take advantage of this offset by living in the nar-row zone where photosynthetically active radiation is high enough to support photosynthesis but ultraviolet radiation is low enough to be tolerable (Belnap et al. 2003).

Boundary function. Boundaries may themselves affect eco-logical phenomena (figure 3; Belnap et al. 2003). Many cases exist in which boundaries transform materials. For instance, many materials are transformed at oxic–anoxic boundaries in groundwaters or where groundwaters discharge into sur-face waters (Chapelle 1993, Phillips 1999). Thus, ammonia may be transformed into nitrate by oxidation at a ground-water–surface water boundary. Similarly, soil crusts transform nitrogen gas and carbon dioxide to ammonia and organic car-bon, respectively (Belnap et al. 2003).

Ecological boundaries are commonly differentially trans-missive or permeable; that is, they may allow only some frac-tion of materials, energy, or organisms to pass. Thus, wind speed falls as it moves from an open field into a forest (Geiger 1965), and many animals are reluctant to cross boundaries (Wiens et al. 1985, Duelli et al. 1990, Fagan et al. 1999, Lidicker 1999). As an extreme case of impermeability, many ecologi-cal boundaries are absorptive: For example, most of the me-chanical energy contained in waves is absorbed in the surf-zone boundary that separates land and water. This absorption of energy concentrates materials along the shore and has profound consequences for the ecology of the beach zone (McLachlan and Erasmus 1983, Polis and Hurd 1995, 1996).

If transmission exceeds 100%, the boundary has amplified the ecological phenomenon. Amplification by ecological boundaries is probably rare. A possible example is when groundwater rich in carbon dioxide passes from carbonate-poor rock (e.g., sandstone) to carbonate-rich rock (e.g., lime-stone). As the water crosses the boundary, the carbon diox-ide aggressively dissolves calcium carbonate from the rock, increasing the content of dissolved inorganic carbon (DIC) in the water. Thus, the DIC vector is amplified by crossing the boundary.

In many cases, boundaries are reflective: Organisms or materials that approach the boundary are returned to the patch from which they originated (highly reflective boundaries are sometimes called hard boundaries; Lidicker 1999, Ries and Debinski 2001). From the viewpoint of a fish, the shoreline (or, in some cases, even the 20-centimeter depth contour) is a reflective boundary (Power 1984, 1987, Power et al. 1989). Like transmissive boundaries, reflective boundaries may at-tenuate or amplify an ecological phenomenon and therefore might be said to have an albedo. (Fish approaching a shore-line where the water is receding may be stranded and killed in shoreline pools; in this case, the shoreline both absorbs and reflects fish.)

Finally, the boundary itself may have no effect on the phe-nomenon under study (a neutral boundary).

Temporal dynamics. Maps or diagrams of boundaries repre-sent snapshots of boundary structure at a given moment; a single map or diagram may give the impression that bound-aries do not change over time. In fact, many ecological bound-aries are dynamic (Fagan et al. 2003). We ask two basic ques-tions about temporal dynamics of boundaries: (1) Are the
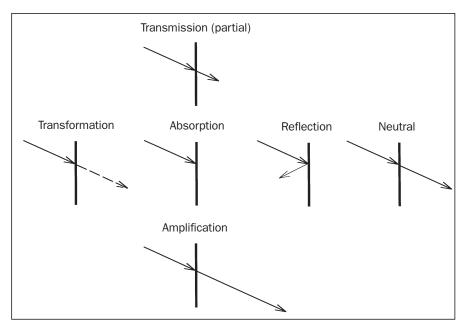
Figure 3. Possible activities of ecological boundaries. The heavy vertical line is the boundary, and the thin arrows are fluxes across, into, or out of boundaries. The length of the arrow indicates the size of the flux.

position, structure, and function of the boundary stable over time? and (2) What is the age and history of the boundary?

Both the properties and the position of a boundary may change over time. Several spatial properties may change: Boundaries may become sharper or more diffuse; conduits may appear or disappear. For instance, vegetational growth along the boundaries of tropical forest patches may make the boundaries less permeable over time and isolate the interior of the forest from the surrounding matrix (edge sealing; Williams-Linera 1990). The position of a boundary in the landscape may be stationary over time, or it may move. Movement may be directional (a forest expanding into a neighboring field, a growing root tip; Belnap et al. 2003), oscillating (a salt front in an estuary moving with tides or with regular seasonal changes in freshwater flow from the watershed), or irregular (a climatically determined boundary between biomes moving in response to a fluctuating climate). Further, a change in the location or properties of a boundary may be predictable or unpredictable.

The age and history of a boundary may also be important. Some boundaries are ephemeral (films around bubbles), while others are ancient (continental margins, boundaries between biogeographic provinces or geologic formations). Because the effects of a boundary may be cumulative, the age and history of a boundary may determine its functional properties and the local ecological conditions around the boundary. The edge sealing described for tropical forest edges may take years to develop (Williams-Linera 1990). Biogeochemical reactions occurring in boundaries may result in the progressive buildup or depletion of materials along the boundary as it ages. Phillips (1999) noted that oxidation of iron seeping from the groundwater through the sides of val-

leys can cause the progressive formation of ferricretes (a layer of hardened iron oxides) along anoxic–oxic boundaries. The amount of ferricrete that is formed depends in part on the age of the boundary. Thus, both the function and the structure of a boundary may depend on its age and history.

Conclusions

Ecologists use the term *boundary* (or *edge)* to refer to a wide range of conceptual and tangible structures. Different ecologists may use *boundary* to mean structures that are two-dimensional or three-dimensional; mental or physical; microscopic to regional in size; step functions or gradients; reflective, absorptive, or permeable; and so on. As long as usage is so varied, it is important for ecologists to specify the type of boundary they are investigating. Our intent in presenting a classification of ecological boundaries is to expose this wide range in usage to critical examination, not to encourage literal, formal classification of ecological boundaries.

Different kinds of boundaries may have very different structural and functional characteristics. Consequently, different kinds of boundaries are as different as apples and oranges, and careless confounding of different boundary types may lead to unfruitful study designs, tests of theories, and comparisons across studies. Ecologists who wish to compare empirical studies of boundaries to predictions of theories, empirical studies to one another, or theories to one another need to be careful that the boundaries defined in these studies are truly comparable. For instance, theories that model boundaries as two-dimensional are best tested with field studies whose design uses a two-dimensional, rather than three-dimensional, approach to boundary definition. Likewise, phenomena such as diffusion, boundary layers, and laminar flow, which may be essential to measure or model in studies of small boundaries, may be dispensed with in studies of large boundaries. Comparisons of many structural characteristics of boundaries (e.g., tortuosity, integrity) must be made using comparable grain sizes. Transport across perforated boundaries may be much higher than predicted by models of unperforated boundaries. These and many other examples show that careful specification of boundary traits can improve understanding of the structure and function of ecological boundaries.

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