A Framework for a Theory of Ecological Boundaries

MARY L. CADENASSO, STEWARD T. A. PICKETT, KATHLEEN C. WEATHERS, AND CLIVE G. JONES

Boundaries are ubiquitous across a wide range of ecological systems and spatial scales. However, most research on boundaries has been scale and system specific. To promote the synthesis of boundary studies across the range of environments and scales they represent, we present an inclusive scope for boundary studies. Three linked tools make the scope operative: (1) a causal framework covering all types of boundaries, (2) a model template, and (3) a strategy for constructing hypothetical models of boundary function in any ecological system. The framework focuses on flows of organisms, materials, energy, or information in heterogenous mosaics; it specifies patch contrast, identity of the flow, and nature of the boundary as the concepts to quantify in any model. The model template arranges these components in a functional form to elucidate specific boundary relationships. From the model template, working models that are system and scale specific can be developed. We exemplify the use of the linked tools of framework, model template, and working model with an experimental study of forest–field boundary function.

Keywords: boundary, edge, spatial heterogeneity, conceptual framework, theory

Boundaries are important components of spatially heterogeneous areas. Boundaries are the zones of contact that arise whenever these areas are partitioned into patches. However, such a concept of boundaries can overemphasize the static or descriptive aspect of boundaries. Therefore, the understanding of how boundaries influence the functioning of ecological systems is poorly developed. When, where, and how boundaries affect ecologically important flows across heterogeneous space is not well known. In addition, the potential for an inclusive and synthetic understanding of boundaries that can bridge ecological specialties and scales has not been explored.

Two recent extensions of landscape ecology help advance the understanding and synthetic value of boundaries. First, the landscape concept can apply at any spatial scale (Allen 1998). Although Forman and Godron (1986) examined landscape ecology at scales of kilometers or larger, the basic idea of spatial pattern as a driver of ecological processes (Turner 1989) is not inextricably linked to coarse scales (Allen and Hoekstra 1992). In fact, landscape ecology is a criterion of observation that focuses on heterogeneity at any spatial scale (Allen and Hoekstra 1992). Second, the landscape concept applies not only to terrestrial habitats but to aquatic and transitional habitats as well. Although many of the examples used in landscape ecology have come from terrestrial habitats (Forman 1995), spatial heterogeneity can be equally important in bodies of water (e.g., Wiens 2002), volumes of soil (e.g., Facelli and Facelli 2002), and land–water transitions (e.g., Polis and Hurd 1996). These extensions of the landscape concept mean that the tools we present here for unifying and stimulating the functional study of boundaries can operate on a vast range of scales and habitat types. Therefore, we use the term *landscape* in a scale- and system-neutral way.

To advance the development of a theory of ecological boundaries, we use as a guide Pickett and colleagues' (1994) clear articulation of the elements of theory and the task each element performs in theory development. We focus on three of those elements: a conceptual framework, a model template, and an approach to developing working models. The task of a framework is to organize the components to be included in the theory and to illustrate their potential relationships. From the framework, a model template to test the effective relationships among the components can be constructed. Finally, a working model, specific to a particular place, scale, and series of questions, must be developed to actually test relationships among framework components. All three tools inform one another. Through testing the working model, additional

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components can be added or removed from the framework, and components can be organized into, for example, functional groups. The framework is not an end point but rather a tool to help create models and generate hypotheses.

The steps outlined above show how to use important elements of theory to advance any area of ecology. Here we apply these steps to the subject of ecological boundaries. We begin by defining and describing patches and boundaries, which are the structural and functional components of landscapes. To make the abstract concepts of patches and boundaries operational for specific, yet diverse, circumstances, we present a conceptual framework for boundaries that can accommodate many ecological systems and scales. We present two central questions that indicate why it is important to consider the function of boundaries in landscapes. These questions identify the scope of the framework, and the framework suggests a roster of potential drivers of boundary function. The framework is used to develop a template for models investigating boundary function. Because the template mirrors the framework and is intended to encompass the range of systems and scales in which boundaries may play a role, the template is necessarily general. Finally, we demonstrate how to develop a working model for a series of specific questions about boundary function. The working model produces novel hypotheses for explaining boundary function. To illustrate, we use the working model to test how forest edges, as a particular boundary type, modulate the flows of organisms and material. The models we present are conceptual or empirical, but analytical models can follow the same format. Combining the linked tools of framework, model template, and working models can promote both unification and comparison in studies of ecological boundaries across a range of ecological systems and scales.

Components of landscapes

Landscapes consist of two kinds of structures: patches and boundaries. Though frequently depicted on maps as two-dimensional, patches and boundaries are three-dimensional, extending above and below the surface.

Patches. Patches are volumes that can be distinguished compositionally, structurally, or functionally from adjacent volumes at a given scale. For example, if a question focuses on forest fragments, then the landscape can be divided into patch types that are forest and those that are nonforest. The patches defined as forest are assumed to be structurally similar and to contrast with the structure of patches defined as nonforest. However, the forest patches are not necessarily internally homogeneous in terms of characteristics such as tree density or species composition.

Patches can be discerned at any scale. For example, at finer scales, research on rock-eating snails in the Negev Desert, Israel, quantified the transfer of nitrogen (N) between patches of endolithic lichens and adjacent patches of soil as a result of the snails' feeding, defecation, and resting (Jones and Shachak 1990). The movement of stream invertebrates among sand and leaf patches within a streambed is another example of fine-scale patches (Palmer et al. 2000). At a coarser scale, patches can be a habitat type such as deciduous forests or prairie, or they can be aquatic or terrestrial systems if the research question addresses cross-system transfers.

What constitutes a patch is determined by the research question and is based on characteristics perceived or postulated to be relevant to the answer. Because patch delimitation is guided by questions, different questions result in different patch arrays, even for the same physical space. For example, a question based on land use may result in a different patch array than a question about forest fragmentation (figure 1).

Boundaries. Boundaries mark patch limits; they are the zones between two neighboring patches. Boundaries are complex and multidimensional, but we suggest six general characteristics:

1. Boundaries may have some characteristics in common with the patches that they separate, or they may be completely distinct.
2. Because the patches that the boundary separates are distinguished from each other by some defining characteristic, the gradient in that characteristic is steeper in the boundary than in either of the neighboring patches.
3. Boundaries may be wide or narrow, depending on the gradient of change between patches.
4. A boundary for one characteristic may differ in magnitude and location from a boundary defined by another characteristic.
5. The function of a boundary is determined by an organism or by material, energy, information, or some process that is affected by the boundary gradient.
6. Boundaries are best construed as three-dimensional.

The contrast between a forest and a meadow exemplifies the nature of gradients as an aspect of boundaries. The most obvious contrasting feature is the presence or absence of a tree canopy, and the boundary represents a gradient of plant architecture. If the meadow is mown close to the forest, the boundary may be very narrow. In contrast, if the meadow is not mown close to the forest, the boundary may be wider and the transition in plant architecture from the meadow grasses to the mature trees of the forest more gradual, as young trees and shrubs become established at the interface. Another gradient across this boundary is the level of light reaching the ground. The shift from high levels of light in the meadow to low levels in the forest may be more gradual than the gradient in plant architecture. Consequently, the boundary for light may be wider than that for plant architecture; although those two gradients may overlap, they need not be exactly congruent (Fortin et al. 1996, Cadenasso et al. 1997).

Specific locations in a landscape can serve as a boundary for one research question and as a patch for a different question. For example, an estuary is a patch for questions about

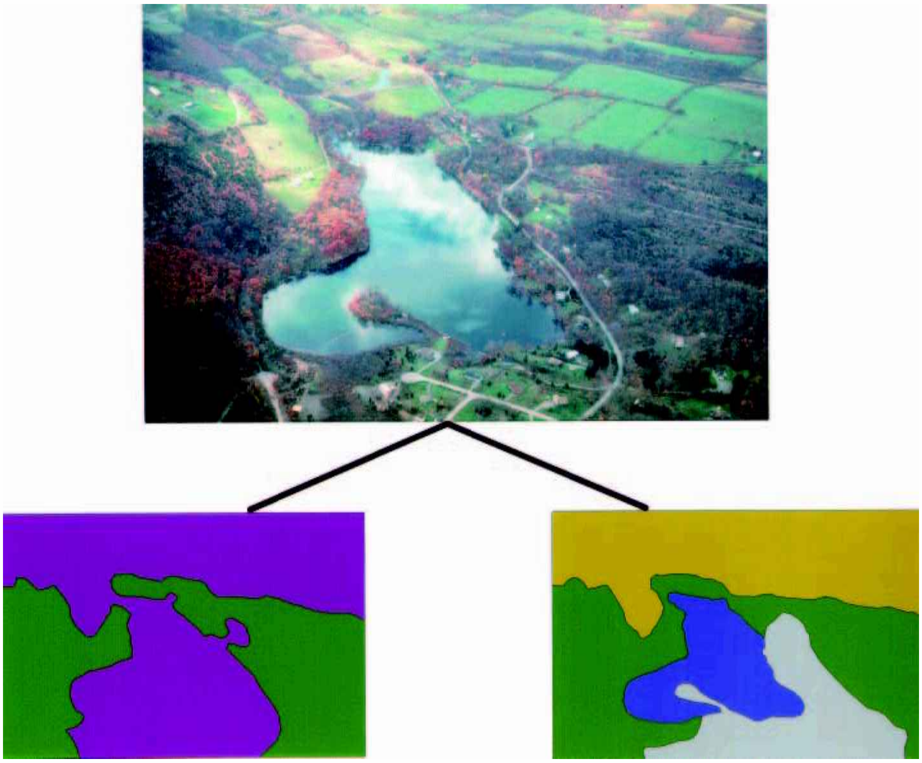

Figure 1. Different patch arrays for the same physical space. The bottom left panel shows an array that may be used to study forest fragmentation; the area is differentiated into patches of forest and nonforest. The bottom right panel array is the same area with patches delineated based on land cover, which is appropriate if land cover is the feature being studied. Photograph: Michael L. Pace, Institute of Ecosystem Studies.

its function as a nursery ground for fish, but it can also be considered to be a boundary between freshwater and saltwater systems for different questions. Similarly, a riparian zone may be a patch in the landscape if the research question focuses on the flow of N within the riparian zone, but it may be a boundary between upslope habitats and the stream if the focus is on the flow of N in groundwater between adjacent uplands and the stream. These examples demonstrate that it is critical to clearly identify patches and boundaries on the basis of the research question.

Developing a framework for ecological boundaries

Boundaries are important structural features in the landscape. In some cases, their importance in regulating flows across the landscape is disproportionate to the space they occupy. Two central questions frame the scope of understanding boundaries: (1) Do boundaries modulate flows between patches and, if so, what is the nature of the modulation and what characteristics of the boundary contribute to that modulation? (2) If the boundary modulates flows between patches, does the modulation influence processes inside the interacting patches?

To address these two questions, it is useful to have a framework that organizes the concepts and data and helps generate hypotheses. Participants in a multidisciplinary workshop (Cadenasso et al. 2003) described the domain of a framework for ecological boundaries as ecologically significant interactions among heterogeneous entities connected by flows of organisms, energy, materials, or information across a differentially permeable or reactive interface at any spatial and temporal scale. From this domain we extract the overarching goal of the framework: *understanding the regulation of flows across heterogeneous space.*

There is a tradeoff between specificity and inclusiveness within a framework, but both can be accommodated by a hierarchical structure. Resolving to the greatest detail describes processes at fine scales and in specific environments, whereas the clustering of detailed, specific processes exposes more general processes. Therefore, to use a general and inclusive framework, a researcher must articulate the spatial and temporal scales to be addressed to know where in the hierarchy to operate (Pickett et al. 1994); as noted above, the research question determines the patch and the boundary. When these determinations have been made, the researcher can turn to the three components of the framework—the type of flow, the nature of the bounded systems, and the nature of the boundary (figure 2).

Type of flow. Four types of flow are relevant to ecological systems: materials, energy, organisms, and information

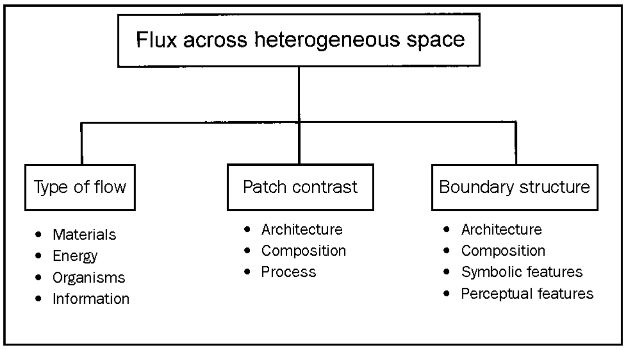

Figure 2. A conceptual framework for ecological boundaries. The framework has hierarchical structure and contains the major processes, system components, and types of system parameters required to understand boundary function at any scale. On the highest hierarchical level, the framework identifies the phenomenon to be understood: flux across heterogeneous space. At the middle hierarchical level, this phenomenon is divided into three contributing components: type of flow, patch contrast, and boundary structure. On the lowest hierarchical level, the elements of these three components are specified for a field situation or model application. The possible detailed variables would be drawn from other relevant theories, both in ecology and in other disciplines.

(figure 2). This list is categorically comprehensive and represents multiple levels of ecological organization, but we will not enumerate all the kinds of flow within each general category.

Flows of materials include nutrients, pollutants, dead organic matter, and clonal plant fragments. Materials move between patches through mechanisms such as diffusion, gravity, and transport by wet and dry deposition, groundwater and surface water, wind, or animals. Animal transport can involve ingestion of material in one patch and excretion or death in another. The flow of materials, including type, amount, and delivery mechanism, varies across spatial and temporal scales.

Energy flow between patches can involve physical dissipation and transformation or movement of stored energy in biological forms. Energetic flows include light, heat, wind, and tides, the latter two of which serve as vectors of organisms and materials. Energy stored in biological forms may move across boundaries. For example, the energy in carbohydrates eaten by an animal in one patch can be dissipated as metabolic heat in a second patch. Similarly, material consumed by an animal in one patch and defecated in a different patch may transport stored energy from the first patch for use by decomposers in the second patch.

The flow of organisms is a higher level of organization than the flow of either matter or energy alone. Organismal movement around the landscape may operate at broad spatial scales, as in the migration of elk herds or songbirds. Organisms may also move shorter distances but still traverse boundaries between patches, as in the daily movement of white-tailed deer between forests and open fields. On still finer spatial scales is the movement of microbes between soil horizons, as well as the vertical movement of pelagic algae. Plants move in landscapes through seed dispersal and clonal spread. The flow of organisms also occurs on many time scales, for example, the use of more than one patch during a life cycle, seasonal or reproductive migration, or diurnal movement in the water column. All of these temporal and spatial scales are accounted for in the framework.

The flow of information encompasses genes and the visual, auditory, and chemical signals that affect pollination, host and mate finding, territoriality, predator avoidance, and so forth. Information is distinct from organisms and material, even though organisms and material may mediate the flow of information. Indeed, for some biological concerns, information is the currency of interest, not the organism or material that carries it. For example, the transmission of the sound of a lion roaring is information for potential prey concerning the whereabouts of the predator. A boundary of vegetation between the lion and the prey may modify or dampen the sound of the roaring, even though the lion did not directly interact with the boundary.

Nature of the bounded systems: Patch contrast. Bounded systems can differ in architecture, composition, or process; the nature of the bounded system defines the characteristic or characteristics used to differentiate patches (figure 2). For example, if patches are described as forest and nonforest, then the contrasting architecture of the plant community defines the patches. Alternatively, research focusing on exchanges between deciduous and coniferous forests may delimit patches based on contrasting species composition. Contrasting composition can also refer to chemical or physical composition, such as the contrast between land and water. The contrasting composition of patches may support different processes. For example, patches of soil may be discriminated based on oxygen concentration, which in turn leads to contrasting processes of aerobic and anaerobic respiration and differences in N dynamics. An open question is how boundaries, defined by contrasts in architecture, composition, and process, are similar or different in structure and function.

Nature of the boundary: Boundary structure. The third component of the framework is the nature of the boundary, which encompasses features of the boundary that influence flows crossing it and, consequently, flows between contrasting patches. A boundary influences flows because of differences in architecture, composition, or symbolic or perceptual features (figure 2). The architecture of a boundary is its three-dimensional structure composed of biological or physical features. Consider the biotic boundary between a deciduous forest and an open field. Fewer seeds traverse the boundary when the forest trees are in leaf than do after the leaves drop in the fall (Cadenasso and Pickett 2001).

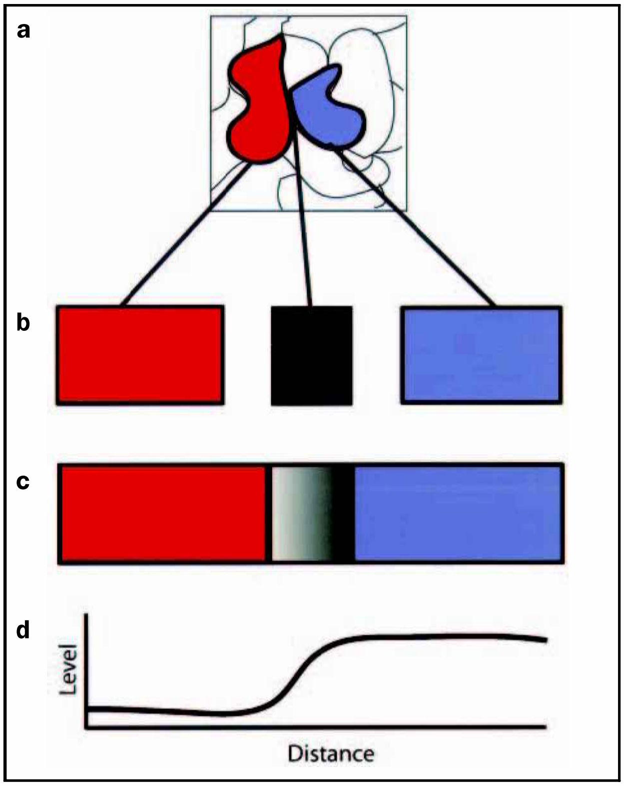

Figure 3. A model template for the study of boundary function. Any model to explain or predict boundary function must specify the boundary of interest, the structure of the patches adjoining the boundary, and the nature and rate of the flows between them. The model template makes the components of the framework (figure 2) spatially explicit and focuses on the interaction of patches through boundaries. The landscape mosaic in (a) consists of patches and boundaries. In (b), two patches—red and blue, with the boundary between them in black—are isolated. The boundary has dimensionality and is the zone of transition between the red and blue patch. The characteristic that differentiates the red from the blue patch changes across the boundary, which is depicted in (c) as the gradient from white to black in the boundary. Panel (d) illustrates that the gradient is steeper in the boundary than in either of the neighboring patches. Specific quantitative or other models to understand boundary function could be developed from this template.

Physical features of boundaries can also modulate flows between adjacent patches. For example, the input of algae from the ocean onto land is much greater on gently sloping shorelines than on steep cliffs (Witman et al. forthcoming). Thermoclines in the water columns of lakes act as boundaries between patches of water, affecting flows of organisms, nutrients, and particles. Organismal movement may be influenced by the gradient in water temperature across the boundary, and the flow of particles may be influenced by the gradient in water viscosity, density, and turbulence. Compositional differences such as those between patches of deciduous and coniferous forests may slow the spread of host-specific pests, or they may be reflected in differences in nutrient cycling rates in the soil. Perceptual and symbolic boundaries include signals—auditory, visual, or chemical—that may indicate to an organism that a predator is nearby or that the territory of a rival troop is being entered.

These examples illustrate how the three components of the boundary framework—type of flow, patch contrast, and boundary structure—can be applied to real aquatic and terrestrial systems across various spatial and temporal scales. Through the development of models, these connections can be made explicit and hypotheses can be generated and tested.

Using the framework to generate a model template

Boundary models express functional relationships among and within the components of the framework. Here we construct a model template for investigating the function of boundaries (figure 3). The template is necessarily general and shows the kinds of relationships that may exist between the components of the framework. It mirrors the conceptual framework and is an abstraction of the two central questions regarding boundary function. The template has two elements: (1) two patches and the intervening boundary and (2) the flows moving between patches and across the boundary (figure 3). This abstraction is necessary because the template serves as a prototype for more specific models (Pickett and Cadenasso 1995). Specific models are derived from different research questions but have the same structure as the general model template.

Boundary function in the model template is purposefully restricted to the level of net effects (e.g., Pickett et al. 1987, 1994). In other words, boundaries can inhibit, facilitate, or be neutral to flows moving across them. Specific processes and mechanisms that account for the net effect are articulated in the next step, the development of working models.

An extreme example of an inhibitory boundary is the water–air interface, which is a barrier to the movement of water-dependent organisms. Similarly, a clay layer in the soil can prevent deep water infiltration. In less extreme cases, boundaries can reduce flows. For example, trees are frequently planted in rows between agricultural crops to reduce soil erosion by attenuating wind energy, and compacted soil layers can reduce rates of water percolation.

Boundaries facilitate flows when the entities entering the boundary leave in a more concentrated form or when the outward flux is greater than the inward flux. For example, populations that can survive and reproduce in the boundary may disperse a greater number of seeds than those entering the boundary from outside.

A boundary can also be neutral to a particular flow. In these instances, either the flow has no net gain or loss as a result of traversing the boundary or the boundary of interest does not interact with it. A focus on net effects does not distinguish between these two types of neutral boundary function (cf. Pickett et al. 1987), but distinction between these types is

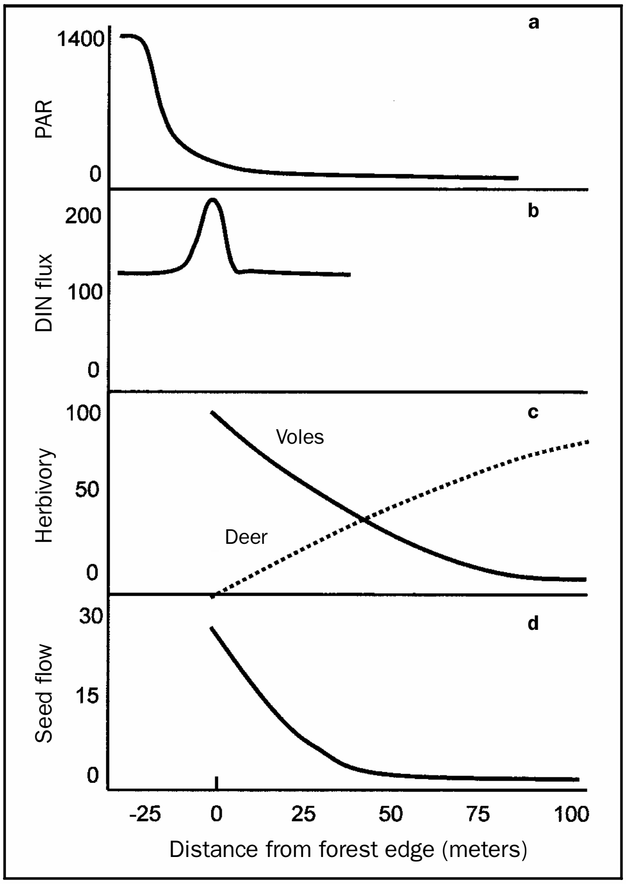

Figure 4. Trends in flows at a forest–field boundary at the Institute of Ecosystem Studies, Millbrook, New York. Distance from forest edge, in meters (m), is relative to 0 (the wall of forest vegetation) at 2 m above the ground, where positive values represent forest positions and negative values represent field positions. (a) Photosynthetically active radiation (PAR) in micromoles per m^2 per second (Cadenasso et al. 1997). (b) Dissolved inorganic nitrogen (DIN) flux in milligrams per m^3. Ambient levels appear in the field, whereas throughfall is measured beneath the forest canopy (Weathers et al. 2001). (c) Percentage of seedlings in the forest understory damaged by voles **(Microtus pennsylvanicus)** *or deer* **(Odocoileus virginicus)** *(Cadenasso and Pickett 2000). (d) Seed flow before leaf drop in autumn, in number per trap line (Cadenasso and Pickett 2001).*

important for understanding how boundary function may change. If neutrality is caused by counteracting flux regulation, a subsequent change may lead to a shift in the net effect from neutral to positive or negative. Mechanistic studies are required to distinguish between the types of neutral boundary function.

Constructing working models from the template

The model template motivates specific working models. For example, we developed and tested a working model for boundaries between deciduous forests and open fields in the Hudson Valley of New York. The two adjacent systems differ from each other both architecturally and compositionally, and the boundary is the zone of transition between the two. The fields have been mown since the 1960s to maintain open space. The adjacent forests, dominated by oaks and maples, are approximately 80 years old. The two central questions concerning boundary function—do boundaries modulate flows between patches, and, if so, does the modulation influence processes inside the interacting patches?—guided the investigation of boundary function in this research. These questions will also organize the following overview of the tests of the working model.

The first question, restated for our working model, is How does the forest edge mediate flows between a forest and a mown meadow? Components of the working model that satisfied the model template and are implied in the question are a spatial scale on the order of meters (m); a boundary anchored on the forest edge; and the neighboring, potentially interacting, patches of forest and field. The gradient in three-dimensional architecture from field to forest was very steep with a sharp boundary. Vegetation on the edge formed a solid curtain, meaning that edge trees had well-developed side canopies, and midstory and understory layers were present. Flows of energy, material, and organisms across the boundary were quantified (figure 4).

Photosynthetically active radiation (PAR) decreased along transects established perpendicular to the edge and extending from 25 m in the field to 50 m into the forest interior (Cadenasso et al. 1997). The flow of dissolved inorganic nitrogen (DIN) was quantified in throughfall (rainfall that had passed through the forest canopy) at the forest edge and the interior and was compared to ambient N deposition in the field. Some gases and particles deposited onto the leaf surfaces during dry days of fair weather, along with what is leached from the canopy, are washed to the forest floor and into the collectors during the next rain. Throughfall is therefore a composite measure of dry and wet deposition and canopy processing. Below-canopy DIN flux was, on average, 50% greater on the edges than in forest interiors (Weathers et al. 2001).

Herbivore damage and seeds were used to investigate the flow of organisms from the field into the forest. The influence of two herbivores, white-tailed deer and meadow voles, on forest regeneration was experimentally quantified by determining the amount of damage each species of herbivore caused to tree seedlings planted at the edge and at 40 m and 100 m into the forest interior. Damage to seedlings by voles was high on the edge and low in the forest; damage by deer showed the opposite trend (Cadenasso and Pickett 2000).

Plant propagule flux was quantified by collecting seeds along transects from 5 m to 50 m into the forest interior. Only seeds of field plants were considered, to ensure that the seeds had in fact crossed the field–forest boundary. The number of seeds trapped decreased with increasing distance into the forest (Cadenasso and Pickett 2001). Clearly, intact forest edges modulate flows of organisms, material, and energy between open fields and forests. Furthermore, the nature and extent of that modulation varies, depending on the type of flow (figure 4).

After determining that this boundary modulates flows, the next question is, What characteristics of the boundary influence that modulation? We hypothesized that the vegetation structure of the boundary interacted with the flows traversing it and, therefore, influenced the nature and magnitude of the modulation. To test this hypothesis, the vegetation structure was experimentally altered by removing all vegetation lower than half the height of the tree canopy, including side branches of the canopy trees up to half the trees' height and complete small trees that were shorter than half the height of the canopy (figure 5). All shrubs were also removed, but the herb layer was not manipulated (see Cadenasso and Pickett 2000 for details).

Flows of DIN, herbivores, and seeds were quantified across the experimentally manipulated boundary. The concentration of DIN was no longer greatest on the edge; now it was higher 25 m into the forest (Weathers et al. 2001). Vole damage to planted seedlings was suppressed on the manipulated edge. In contrast, deer damaged more seedlings on the manipulated edge than on the intact edge (Cadenasso and Pickett 2000). Finally, many more seeds moved across the manipulated edge than across the intact one, and those seeds that crossed the manipulated boundary traveled farther into the forest (Cadenasso and Pickett 2001). All results demonstrated that the vegetation structure of the boundary influences both the capacity of the boundary to modulate flows and the nature of that modulation.

The second central question embodied in the framework is whether the modulated flows influence ecological processes in either the field or the forest. The studies we are using as examples have not yet provided answers to this second question. However, the experiment does indicate that dynamics in the forest may be altered as a result of the boundary's influence on cross-system flows. Three results in particular support this expectation. First, herbivore damage to seedlings was altered when the vegetation structure of the boundary was changed. Voles damaged fewer individuals in the manipulated boundary than in the intact boundary. Because deer and voles selectively damage species and because their damage differentially influences seedling survival, we expect that the dynamics of the regenerating community will be altered by the change in boundary structure. The second supporting result is that intact forest edges enhance the deposition of DIN. This enhancement may cascade through the system and influence interior forest dynamics. Finally, the flow of seeds from the surrounding landscape into the forest interior was influenced by the structure of vegetation on the forest edge. This may have implications for forest structure and dynamics if the seeds are of species that can survive and establish in the interior.

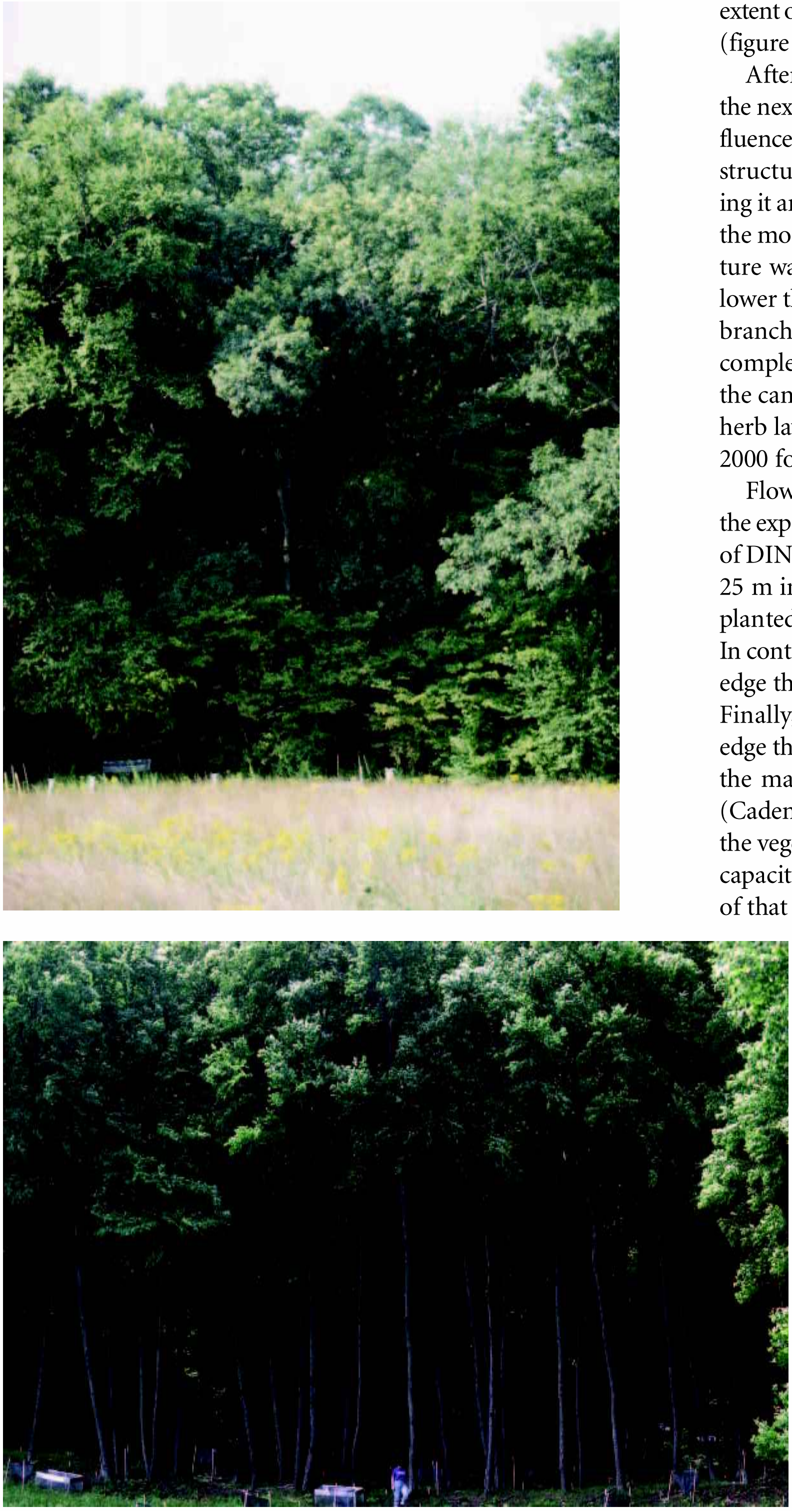

Figure 5. Forest edges with contrasting architectures. The panel on the top is an intact deciduous forest edge with a solid curtain of vegetation. In the bottom panel, the vegetation structure of the edge has been experimentally manipulated. All vegetation lower than one-half the total height of the canopy was removed. This included side branches of the canopy trees, whole trees shorter than one-half the total height of the canopy, and shrubs. The two boundary architectures are in the same continuous edge and are separated from each other by a 20-meter buffer zone.

The series of experiments carried out on boundaries between deciduous forests and open fields indicated how the boundary framework, model template, and a working model are linked and can be applied in a specific system and scale.

Conclusions

We have presented three linked tools for advancing and synthesizing research on ecological boundaries across multiple systems and scales. First is a framework that identifies the basic motivation for boundary research as the regulation of flows across heterogeneous space. A model template, the second tool, can be used to apply the components and their specific mechanisms to a given research or simulation project. The template suggests how to relate flows, boundaries, and patch contrasts in the real world. Finally, a working model developed from the model template and the framework specifies the parts and connections in a given case by articulating the important interactions and flows. Frameworks and models are used together, complementing each another.

We offer the caveat that not all boundaries will be significant for all flows, scales, or systems. However, in many situations, whether or how the structure and configuration of boundaries matters for the dynamics and persistence of a spatial mosaic is an important research topic.

We have identified several key requirements for using a framework and model template to develop working models:

- Frameworks and models are tightly interlinked as part of the same hierarchy of understanding. They are commonly used simultaneously by researchers who may not recognize their distinctive characteristics and roles. However, it is important to keep the two distinct, because the testing of models helps to clarify frameworks. Testing may show that a specific working model is not supported, but the framework is rarely discounted in its entirety. Instead, model failure frequently suggests possible modifications to the framework. The new boundary framework articulated here should be improved as working models are tested in the future.
- A domain for a working model must be specified so that it is clear what parts of the framework should be included in that model. The domain for a model cannot be more inclusive of phenomena than the domain specified for the entire framework. Models are hierarchically nested within the framework.
- The entire roster of phenomena possible for each component of the framework need not be incorporated into any single model. Instead, the user may choose among the phenomena that relate to a particular research question, focal system, process, and scale. Many different working models can be developed from the framework. As hypotheses are tested and understanding grows, additional phenomena may be added to the roster under each component of the framework.
- Working models can be built from any part of the framework. That is, any flow, specific boundary, or contrasting set of interacting patches can serve as the starting point for constructing a working model. However, a complete working model will include variables representing all three components from the general template.

There is a plethora of open questions for future research on boundary function. Are there systematic and predictable differences in how structure-, composition-, and process-derived boundaries modulate flows? Are there fundamentally different types of flows and hence fundamentally different interactions with boundaries? Can flows be categorized by type, such as mobile behavioral entities, passively mobile organisms, chemical processes, energy, or information? These categories represent the content of a flow, which can be either conserved, dissipated, or transformed, and passive or active vectors that may carry the flow (Strayer et al. 2003). Determining whether there are important consistencies and differences among classes of flows and boundaries will further the goal of developing a general theory of ecological boundaries. Comparing the structures and functions of boundaries across diverse ecological scales, and across diverse systems, can promote syntheses and comparisons that will enrich our understanding of boundaries across the entire scope of ecology.

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