Integrating Edge Detection and Dynamic Modeling in Quantitative Analyses of Ecological Boundaries

WILLIAM F. FAGAN, MARIE-JOSÉE FORTIN, AND CANDAN SOYKAN

Habitat boundaries profoundly influence the structure and function of landscapes, influencing ecological processes both locally and over larger scales. In addition, boundaries themselves are dynamic entities whose changes can influence diverse populations, communities, and ecosystems by way of feedback effects. These two issues, scale dependence and spatiotemporal dynamics, underlie much of the now considerable attention that modelers and statisticians have devoted to the quantitative study of ecological edges and boundaries. We present the linkages between methods of delineating boundaries, monitoring boundary changes, and modeling edge-related dynamics. In the process, we clarify statistical and mathematical approaches to the study of ecological edges and boundaries, and we discuss important remaining issues in the area of quantitative edge research. In particular, we address conceptual and methodological problems faced by statisticians and modelers, while highlighting topics that would benefit from a collaborative approach.

Keywords: boundary dynamics, edge detection, edge-mediated effects, modeling, spatial statistics

Discussed variously in terms of edges, ecotones, borders, and boundaries, the generalized concept of ecological boundaries has received considerable research attention over the past decade (e.g., Chen et al. 1992, Hansen et al. 1992, Gosz 1993, Risser 1995, Saunders et al. 1999). For the purposes of this article, we define *boundary* as a zone between contrasting habitat patches that delimits the spatial heterogeneity of a landscape (Cadenasso et al. 2003). Boundaries are specific landscape features that can possess diverse structural properties (e.g., open or closed, crisp and sharp or gradual and fuzzy, straight or sinuous; see Strayer et al. 2003). We use the term *edge* to refer to a sharp boundary, whereas we use the term *boundary* to encompass both sharp boundaries (edges) and those with more gradual structure. Increasingly, scientists' attention has turned from describing boundaries to investigating their functional importance (Didham et al. 1996, Fagan et al. 1999, Laurance et al. 2001), as when edges influence material flows across a landscape (Wiens 1992), provide or limit wildlife habitat (Woodroffe and Ginsberg 1998), or serve as a barrier to movement (e.g., Bider 1968).

Human activities strongly influence the extent and type of boundaries found on Earth. These anthropogenic impacts are increasingly being seen in a dynamic context, and this new perspective has led ecologists to at least two key insights. First, boundaries have both local and long-distance influences, affecting the structure of adjacent habitats and the processes operating in these habitats and in habitats remote from the boundaries themselves (Laurance et al. 1997, Woodroffe and Ginsberg 1998, Saunders et al. 1999, Cadenasso and Pickett 2000). Second, boundaries are themselves dynamic entities, with the potential to vary both spatially and temporally (Wiens et al. 1985, Williams-Linera 1990, Forman 1995), as when the structure of boundaries changes during succession (e.g., Matlack 1994). Given the complexities inherent in this dynamic view of ecological boundaries, quantitative frameworks can significantly enhance our understanding of boundary structures, functions, and consequences.

Historically, studies of ecological boundaries have typically adopted either pattern-based or process-based perspectives, though the interrelationships between structure and function

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are increasingly recognized (Laurance et al. 2001). In some ways, the distinction between pattern and process is reflected in quantitative ecology. Those interested in edge structure (e.g., how boundaries give rise to landscape patterns) often rely on edge-detection methods, whereas those interested in boundary function (e.g., how cross-boundary flows mediate ecosystem processes) typically adopt dynamic modeling approaches.

Conducting quantitative studies of the interaction between boundary structure and function presents the challenge of integrating boundary detection and dynamic modeling. Though rarely employed to date, such methodological integration will be essential to fully understanding complex issues in landscape change, such as the long-term effects of constructing roads and power lines through undeveloped habitats (e.g., Schneider et al. 2003). Given the importance and difficulty of such problems, the purpose of this article is twofold. One objective is to present the linkages between methods of delineating boundaries, monitoring boundary changes, and modeling edge-related dynamics and, in so doing, to clarify mathematical and statistical approaches to the study of ecological edges and boundaries. A second objective is to show that the unification of boundary detection and modeling requires bridging the chasm that separates the concepts of edge structure and edge function. In discussing this integration, we aim to identify opportunities for novel research endeavors.

Boundary structure and function in quantitative research

On structural grounds, Risser (1995) divides ecological boundaries into two major categories: those caused by steep gradients in physical environmental variables and those caused by threshold or nonlinear responses to gradual environmental gradients (figure 1; Strayer et al. 2003). Most discussions of boundaries address patterns and processes associated with steep gradients. Although it is less intuitively obvious, ecological boundaries may also be the product of nonlinear ecosystem behavior, wherein gradual changes in environmental variables elicit dramatic changes in population and community variables when thresholds are reached (Vandermeer and Yodzis 1999). O'Neill and colleagues (1989) describe boundaries that respond in a nonlinear fashion to gradients as "metastable," meaning that ecological properties of the system remain stable only over a limited range of conditions. Metastability has an important practical consequence: Ecologists cannot assume that abrupt changes in populations or communities are the result of large changes in landscape variables.

The distinction between boundaries associated with steep environmental gradients and those that are metastable is especially pertinent to the detection and monitoring of boundaries using spatial statistics, because statistical approaches to boundary detection depend heavily on large magnitudes of change in variables (i.e., strong differences in the variables' quantitative value) as guides to the location of boundaries (Jacquez et al. 2000). Consequently, metastable boundaries—in which changes in response and causative variables are coupled in a nonlinear, often nonobvious, fashion—pose important challenges to statistical research on boundaries (figure 1). The investigation of metastable boundaries constitutes one research area in which integration of dynamic modeling with statistical detection would be especially fruitful. Another area that would benefit from an integration of statistical boundary detection with mathematical modeling of ecological boundaries involves situations wherein factors that created a boundary may not necessarily be the ones that maintain it (see Strayer et al. 2003 for examples).

In contrast to the primarily structural approaches discussed above, Forman (1995) suggested a five-part functional categorization of boundaries: habitat, filter, conduit, source, and sink. For example, the permeability of boundaries to biotic and abiotic vectors can reflect their function as filters (Wiens 1992), whereas by facilitating movement parallel to (rather than across) a boundary, the boundary may serve as a conduit (Bider 1968). Such functional roles are typically studied using dynamic modeling, as described below. Though most dynamic modeling approaches help us understand how boundaries influence population dynamics, community structure, nutrient cycling, productivity, and other ecological attributes in the adjacent patches (Wiens et al. 1985, Naiman et al. 1988, Wiens 1992), they are incomplete because they do not consider dynamic features of the boundaries themselves (e.g., feedbacks that alter the location or characteristics of the boundaries). In particular, monitoring boundaries over time using statistical methods to gauge their resistance and resilience in the face of altered climate regimes or other environmental changes (Hansen et al. 1992) is typically decoupled from dynamic modeling efforts. Such problems constitute a core area that could benefit from increased integration of statistical and dynamic perspectives.

The importance of scale in detecting boundaries

Boundaries can be detected at any spatial or temporal scale, because different patterns emerge at different scales of investigation (e.g., Gosz 1993). Our ability to recognize what is or is not a boundary will therefore change with scale (Wiens 1992, Fortin et al. 2000, Csillag et al. 2001, Cadenasso et al. 2003). Consequently, ecologists must select scales of measurement appropriate to the particular goals of their studies (e.g., Gosz 1993, Fortin et al. 2000). It is also important to realize that boundary structure and function are context-dependent; one cannot fully characterize a boundary without characterizing adjacent patches.

Two interrelated aspects of scale that affect the accuracy of the delineated boundaries and their features need to be considered when designing a sampling regime for detecting boundaries. These are the spatial extent of the study area and the grain (i.e., resolution) of the sampling unit (Fortin et al. 2000, Strayer et al. 2003). For example, the extent of the study area should be large enough to ensure sufficient data collection in adjacent patches as well as within the boundary itself (especially when a boundary is wide, gradual, and

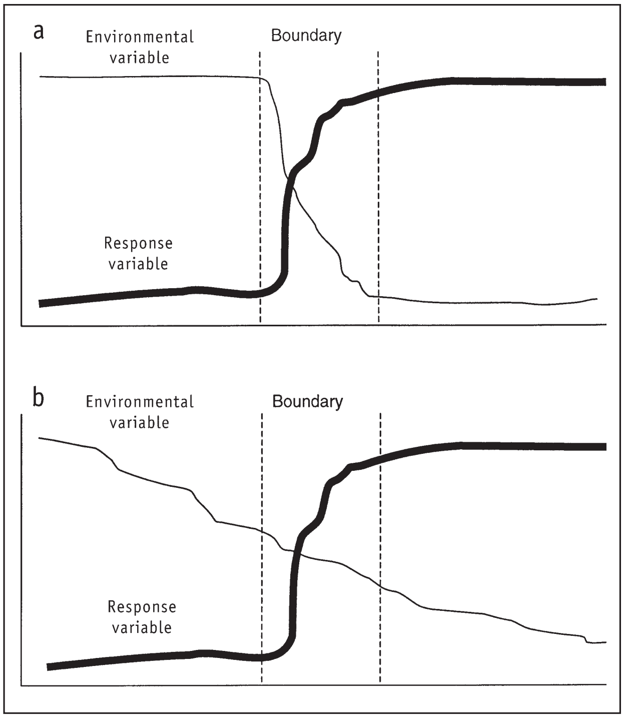

Figure 1. Spatial pattern of environmental variables creating ecological boundaries: (a) steep gradient in the environmental variable; (b) gradual environmental gradient causing either a threshold or a nonlinear response.

sinuous, as are boundaries generated by fire or insects). Furthermore, if the extent of the study area is too small, insufficient pattern exists in the data to permit identification of the boundary's location. In contrast, if the extent is too large (as is often the case with satellite imagery), a different problem emerges, in that multiple ecological processes can each contribute to the generation of edges. This results in "noisy" signals that reduce the ability of statistical boundary detectors to delineate patches' boundaries accurately (Csillag et al. 2001).

Indeed, in edge detection, designing an effective sampling strategy is a difficult problem. A key difficulty is that the most straightforward approaches (such as a systematic sampling design with a standardized spatial lag between sampling units) are not recommended for boundary detection, because mismatches between lag size and system characteristics can result in misidentified boundary locations and misestimated boundary characteristics (e.g., width and shape). Instead, sampling designs that have contiguous sampling units, such as transect (one-dimensional) or lattice (two-dimensional) methods, are more appropriate for characterizing boundaries. Lattice data are especially advantageous because they cover a large area with spatially adjacent sampling units, and boundaries can be detected using either image segmentation or other statistical techniques (Lillesand and Kiefer 1994, Fortin et al. 2000).

The resolution or grain of the sampling unit determines the smallest spatial resolution at which boundary locations can be delimited. At the landscape scale, boundaries can be detected using a remotely sensed image in which the sampling unit size is externally imposed by the pixel resolution of the sensor and satellite (Fortin et al. 2000). It is unlikely, however, that the pixel resolution will perfectly match the ecological process of interest; this mismatch will affect boundary detection. Ideally, the sampling unit size should be large enough to contain more than one individual of interest (e.g., a tree) but small enough to allow edge determination. Clearly, there is a component of art in the science of edge detection. In the following section, we outline different boundary detection techniques and identify the situations in which they are most useful.

Disentangling a web of statistical techniques

A boundary can be defined as a spatial location where the difference (i.e., the magnitude of change) between quantitative values of a variable at adjacent locations is greatest (Fortin et al. 2000). Given the various possible structural attributes of a boundary (sharp, gradual, open, closed, sinuous, straight), the most important quality a boundary detector should have is the flexibility to characterize diverse structural boundary features. A diverse array of statistical boundary detectors has been developed, in part to accommodate a variety of data types and sampling regimes (figure 2) and in part because statisticians have approached the problem of boundary identification from two different directions. The first family of methods groups sampling units into spatial clusters (i.e., patches) based on similarities in variables. This process creates sharp boundaries between the spatial clusters (Fortin and Drapeau 1995, Jacquez et al. 2000). Spatial clustering offers

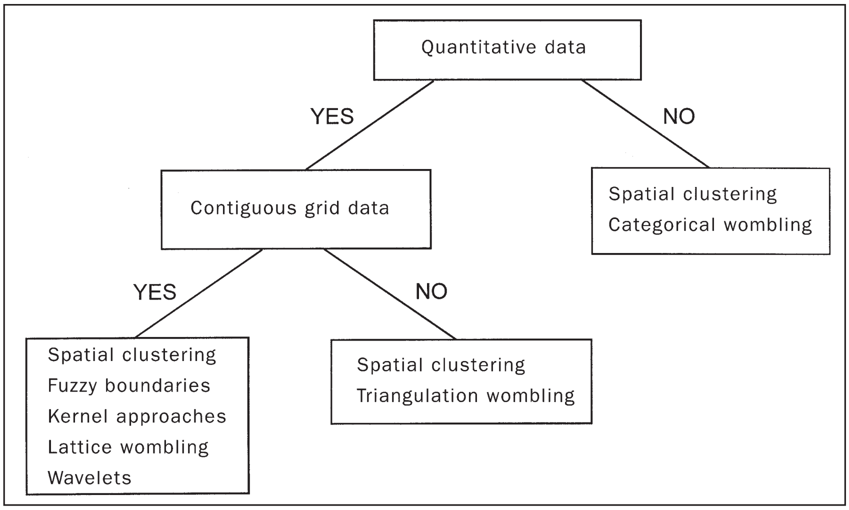

Figure 2. Flow diagram classifying statistical boundary detectors according to data type.

a number of advantages: It can be used with data that are quantitative or qualitative, univariate or multivariate. Further, it completely divides the study area into patches (figure 3a). The major disadvantage of this method is that it delimits only sharp boundaries, which may not reflect the reality of the study area. Because natural boundaries are not always sharp, fuzzy set modeling is increasingly used to identify boundaries when the patch membership of sample points is considered a probability (instead of an all-or-nothing trait) (Leung 1987, Burrough and Frank 1996, Jacquez et al. 2000). The major difficulty with this approach, however, is that the underlying fuzzy membership function is user-defined, and slight changes in this function can drastically affect characteristics of the detected boundaries (Burrough and Frank 1996).

The second family of boundary detectors uses a partition approach. This separates adjacent sampling units based on their degree of difference, with boundaries corresponding to locations that feature high rates of change (Fortin et al. 2000, Jacquez et al. 2000). In this approach, resulting boundaries can be sharp or gradual. These rates of change are computed locally using a "kernel" (i.e., a window of $n \times n$ cells such as 2×2 or 3×3); the rate of change computed is assigned to the center of the kernel. Rates of change can be computed by these kernel detectors either as absolute differences or as gradients using first (e.g., lattice wombling; figure 3b) or second partial (e.g., Laplacian; figure 3c) derivatives among adjacent sampling units (Lillesand and Kiefer 1994). However, kernel detectors are sensitive to local noise between adjacent sampling units, leading to the delineation of artificial boundaries within patches (Csillag et al. 2001). Such local noise can be minimized by using special statistical filters or by increasing the size of the kernel (e.g., 5×5, 7×7; Lillesand and Kiefer 1994). When noise is present at both local and regional scales, the most efficient boundary detection approaches also have hierarchical characteristics. Hierarchical methods (which have names like "quadtrees" and "wavelets") are less sensitive to noise because they can compute boundaries at several scales by varying the size of the kernel. Also, using a hierarchical approach, the locations of delineated boundaries can be optimized to achieve a user-defined number of patches (Csillag and Kabos 2002). Wavelet techniques are increasingly available in software packages (e.g., geographic information systems, or GIS) and should see greater usage because of their robustness to noise and their flexibility in employing diverse kernel functions for boundary detection. However, to take advantage of such flexibility, users must be knowledgeable about the underlying methodological details.

When available data are quantitative but are sampled using an irregularly spaced design (e.g., random, stratified, systematic triangular), traditional partition-type boundary detectors, using square kernels, cannot be used. Instead, researchers can use triangulation wombling, based on a triangular kernel. Trios of sampling units can be obtained by creating a so-called Delaunay network that links adjacent sampling units into triangles (figure 3d; Fortin and Drapeau 1995). Finally, with categorical data, boundaries can be detected using categorical wombling as a "mismatch" where two adjacent sampling units belong to dissimilar categories (figure 3e; Fortin and Drapeau 1995, Jacquez et al. 2000). Categorical wombling performs better when several categorical variables are available for analysis; boundaries correspond to locations where multiple variables exhibit mismatches between adjacent samples. This ability to integrate across multiple variables is a key advantage of categorical wombling (and other wombling approaches) over kernel detectors and wavelet approaches, which find boundaries using only a single variable (Jacquez et al. 2000).

Despite the inherent flexibility of these approaches to edge detection and their powerful opportunities to match statistical techniques with data types (e.g., categorical wombling for categorical data), they have two major drawbacks. First, because boundaries are based on rates of change, users need to define the threshold at which the rates of change constitute a boundary. Such thresholds are often set arbitrarily, although users can reduce the arbitrariness of their decisions by choosing thresholds that break the study area into a specific number of patches (Fortin and Drapeau 1995). Second, statistically identified boundaries are not necessarily significant ones; an identified boundary may not be significantly more pronounced than the interpatch differences that could be expected to occur by chance. Procedures to test the significance of these boundaries are still inadequately developed.

The statistical significance of boundaries. It is important to discriminate between boundaries that are real features of a landscape (i.e., are spatially cohesive and connected; figure 4a) and those arising from random chance (i.e., disconnected locations that have high rates of change but are scattered across the study area; figure 4b). Randomization procedures are one possible way to test whether observed boundaries are cohesive and significantly different from those generated by completely randomizing the data. However, randomization tests for boundary significance must be conducted carefully, because data sampled within patches and across edges are not spatially independent, a consequence of within-patch spatial structure and autocorrelation generated by ecological processes (e.g., seed dispersal, soil moisture). Although complete randomization procedures generate small, isolated boundaries, their magnitudes are often larger (figure 4b) than those observed in the original data (figure 4a). Hence, to test the significance of boundaries, a better option is to use restricted randomization procedures that place spatial constraints on the degree to which sample points are reshuffled (Fortin et al. 1996). For example, the randomization can be restricted within patches (figure 4c) or otherwise matched to the degree of spatial structure in the data (Jacquez et al. 2000).

Monitoring the position and influences of boundaries. After statistically significant boundaries are identified, functional relationships between boundaries can be analyzed using overlap statistics that, roughly speaking, provide a measure

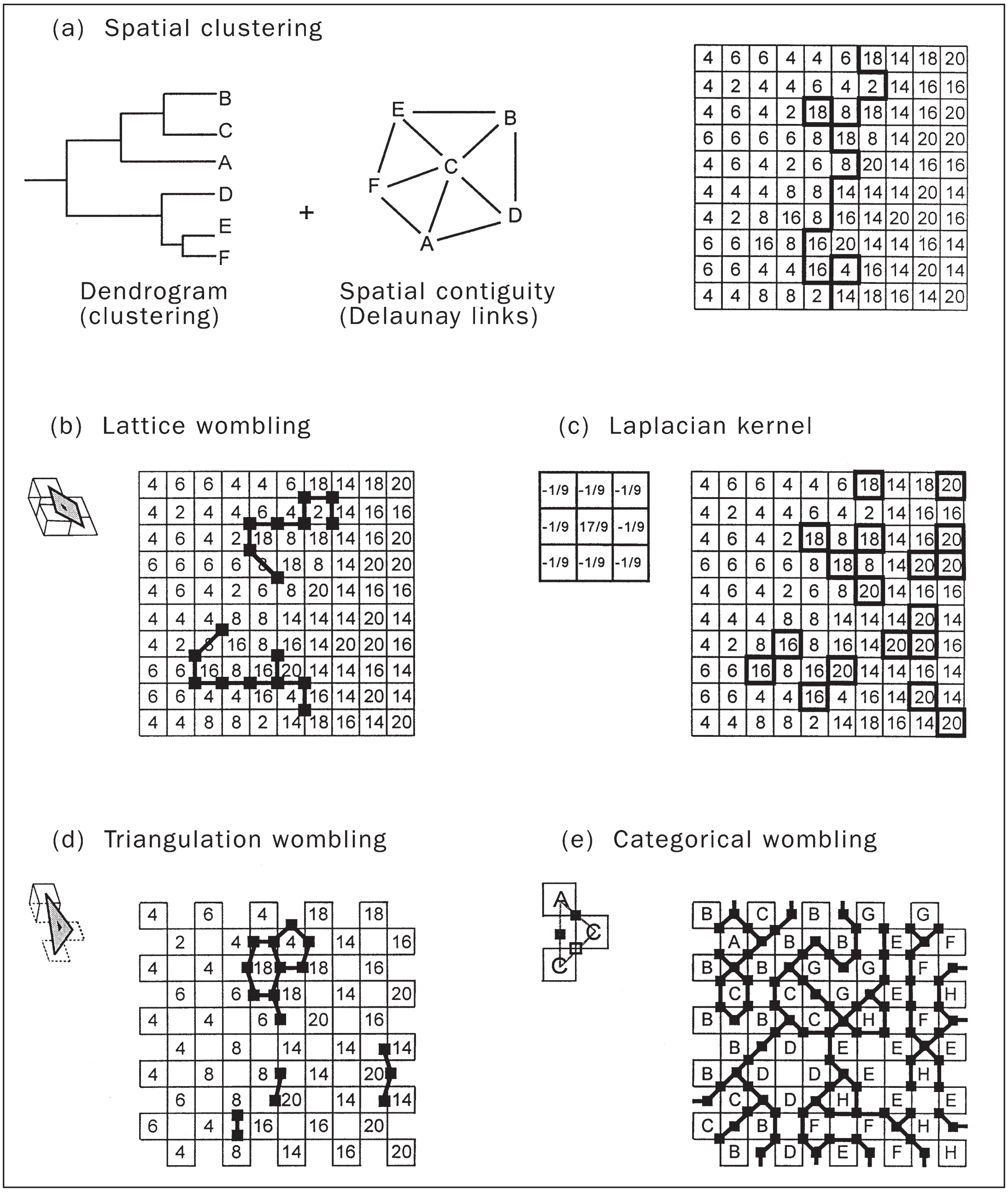

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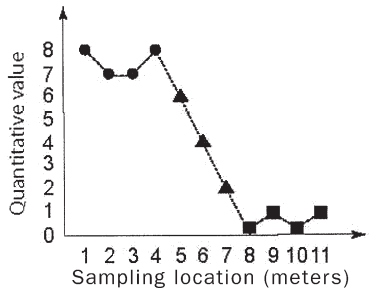
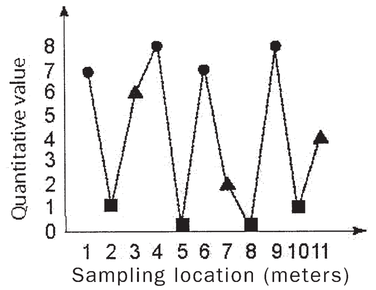
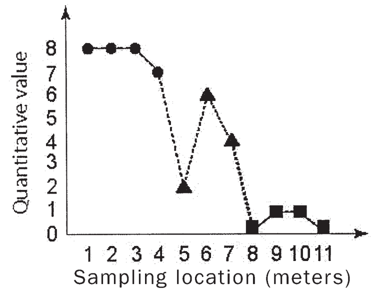
Figure 3. Examples of how statistical boundary detectors work. The square grids with numbers inside each cell represent a landscape of sampled data (e.g., from a ground survey or satellite image). The bold lines indicate the boundaries defined on the landscape according to each statistical technique. (a) Standard spatial clustering techniques require a dendrogram defining the quantitative similarity of sampled points and a map that characterizes their spatial contiguity (here defined using Delaunay links). Four patches were needed to separate the study area into two habitat types, because two isolated samples were extremely different from their surroundings. (b) Lattice wombling computes the rate of change among four adjacent cells forming a square and assigns the rate to the midpoint rather than to a cell. Defining boundary units as the highest 20% of the 81 calculated rates of change on the grid, 17 midpoints are identified (the filled black squares). Connecting these to each other by nearest neighbor methods yields two discrete boundaries. (c) A Laplacian kernel determines the difference of the central cell and each of its eight neighbors using a 3 x 3 cell kernel. These differences are multiplied by the value of the respective neighboring cells, summed, and then assigned to the central cell. Applying the same 20% threshold (20 rates of change out of 100) yields eight boundaries (nine total patches). (d) Triangulation wombling computes rates of change among three adjacent cells forming a triangle. Applying the same 20% threshold (17 rates of change out of a possible 80) yields four boundaries. (e) Categorical wombling computes mismatches between pairs of cells for some categorical trait. All the mismatches are shown and, when linked, give four boundaries.



(a) Observed quantitative data along a transect



(b) Example of complete randomization



(c) Example of restricted randomization

Figure 4. Significance tests for boundary based on randomization. (a) Observed values of a quantitative variable at sampling locations along a transect across two patches (patch A, circles; patch B, squares) and the boundary between them (triangles). Differences (rates of change) are indicated by the lines between the values at the sampling locations. (b) The rates of change generated by complete randomization are higher than those for the observed data. This is because the complete randomization procedure thoroughly disrupts the spatial configuration of the samples, shuffling and intermingling the observed values so that a high value from patch A can be next to a low value from patch B. Thus, the complete randomization procedure does not accurately represent the spatial structure of the data and the underlying ecological processes. (c) Restricted randomization, in which sampled values are reshuffled within, but not among, each patch and the boundary, preserves the spatial structure of the data and the underlying ecological processes.

of how boundaries are positioned relative to one another (Fortin et al. 1996, Jacquez et al. 2000). Though still several steps away from the cause-and-effect insights that dynamic modeling can provide, overlap statistics allow researchers to test such interesting questions as "Is the location of a forest boundary associated with the location of a hydrologic boundary?" and "Is the position of a boundary moving through time?" Two types of overlap statistics exist: (1) the direct overlap statistic, which counts the number of times the edges are at the same location; and (2) the minimum nearest distance statistic, which computes the average minimum distance between two boundaries. Restricted randomization tests should also be used to test the significance of these overlap statistics (Fortin et al. 1996).

In other cases, the goal is not to identify links between the spatial positions of different types of boundaries but rather to test for the effect of the location of a boundary on some other ecological variables, such as seedling density or degree of nest predation. In such cases, one may wish to establish how extensive such edge effects are by using measures like the depth or area of edge influence (Chen et al. 1992, 1996, Saunders et al. 1999, Harper and Macdonald 2001). These methods first compute a reference distribution of the ecological variable in a control area (e.g., nest predation rate in a forest) and then quantify how the variable deviates from the reference distribution at increasing distances from the boundaries. Spline analyses, such as that conducted by Cadenasso and colleagues (1997), can also be used to determine the spatial co-occurrence of gradients of abiotic variables across boundaries. Regardless of the statistical approaches used, it is in considering the spatial co-occurrence of boundaries, and the functional relationships among these boundaries, that conceptual edge detection issues come closest to those involved in dynamic modeling of edges.

Dynamic modeling of boundary-mediated processes

Modeling approaches that treat boundary-related dynamics fall into three broad categories, presented here in order of increasing complexity and realism: (1) implicitly spatial models with spatial heterogeneity, (2) process-based engineering models focusing on the details of boundary flow, and (3) explicitly spatial models incorporating geometric detail. Of course, other spatial modeling approaches, such as metapopulation theory, also deal with issues and processes in which boundaries play vital roles. However, we focus our overview here on modeling methods for which the consequences of boundaries are of primary concern.

The first category of models includes those in which space is treated implicitly and the impacts of boundaries on ecological processes of interest are modeled indirectly. For example, simple patch models may assume that emigration across a boundary occurs and that some of the migrants are lost. Likewise, spatial subsidy models assume continuous or pulsed inputs of nutrients, materials, or species from outside a domain of interest (e.g., Huxel and McCann 1998). The impact of the boundary, which mediates and may ultimately control such flows, manifests itself only indirectly. Such implicitly spatial models sacrifice detailed descriptions of cross-boundary dynamics in favor of more general study of heterogeneous patches coupled by dispersal. This approach is advantageous when changes in boundary characteristics are only of secondary interest.

In contrast, the second and third classes of models involve approaches that deal explicitly with boundary conditions and therefore require more detailed mathematical representations of how a boundary disrupts, modifies, or otherwise influences ecological processes of interest (e.g., dispersal, nutrient flow). For example, the second class of models includes applications of models from fluid dynamics that attempt to capture the details of cross-boundary and near-boundary flows. Typically, these models adopt a small-scale perspective, such as the boundary dynamics of individual coral heads (Thomas and Atkinson 1997). However, because this modeling approach places a special emphasis on the study of mixing processes, it could, if applied at larger scales, provide insights into the influences of wind damage on boundary structure (e.g., Laurance et al. 1997) and turbulent flow on the dispersal of nutrients, seeds, insects, and other airborne materials (e.g., Weathers et al. 2001). Thus, at larger scales, engineering models or other approaches that explicitly deal with physical processes may afford unique insights into the contributions of boundaries to the maintenance of landscape heterogeneity.

The third class of theoretical approaches involves spatial models that emphasize aspects of habitat geometry and connectivity. Mathematically speaking, a diverse array of models would fall within this class of approaches, including both spatially explicit population models (SEPMs; Dunning et al. 1995) and partial differential equation models (PDEs; Holmes et al. 1994). These two modeling frameworks are at opposite extremes in terms of the way they attempt to capture the details of habitat geometry. For example, SEPMs can involve computer simulations of animals moving around in alternative landscapes where multiple habitat patches and boundaries are specifically delineated and may determine dispersal rules. In practice, such detailed models are usually invoked when researchers want to answer very specific questions about the influences of landscape structure on population dynamics, such as how specific arrangements of patches, edges, and the surrounding habitat affect persistence at the landscape level. Such detail is not uniformly advantageous, as in cases explored by Wennergren and colleagues (1995) in which uncertainty in dispersal parameters for SEPMs resulted in highly variable and weakly predictable population dynamics.

In contrast, PDE formulations of boundary-related questions typically specify little more than the existence of one or more patches with certain geometric properties, a boundary that influences dispersal in particular ways, and perhaps some habitat heterogeneity manifesting as a quality gradient (e.g., Fagan et al. 1999). Despite their simplicity, PDE models can incorporate attributes of both patch structure and boundary dynamics; as a result, they lend themselves to investigations of a variety of spatial issues. They are particularly useful for asking generic, conceptual questions about the influence of spatial or geometric factors on population dynamics or species interactions, rather than for trying to understand the detailed dynamics of a specific system or landscape.

For example, PDE models can be formulated to ask questions about critical patch size. In such cases, the goal of the modeling is to identify threshold conditions under which a species' intrinsic population dynamics, or impacts from another species (e.g., predation; Cantrell et al. 2001a), will cause the extinction of the focal species or prevent its colonization. Similar approaches could be used to investigate the patch dependence of ecosystem processes (e.g., the fixation and loss of nitrogen). A variant on the critical patch size theme involves some kinds of spatial control problems. Frequently the term *spatial control* is used in connection with large-scale manipulations of landscape heterogeneity to achieve some desirable result, such as the prevention of insect outbreaks (e.g., rice pest reduction; Settle et al. 1996) or the persistence of species or habitat types (e.g., forest landscape management; Cissel et al. 1999). However, similar concepts can sometimes be studied using simpler patch-boundary problems. For example, Ludwig and colleagues (1978) modeled a case in which patch size could be manipulated to prevent the spatial spread of insect outbreaks.

A second area of PDE modeling includes boundary hostility problems. In boundary hostility problems, patch attributes are held constant, but the nature of the boundary (or characteristics of the boundary resulting from the difference between a patch and the surrounding matrix habitat) is allowed to vary. This kind of modeling has been used to ask a variety of questions associated with nature reserves and other aspects of conservation biology (Fagan et al. 1999). For example, Cantrell and colleagues (2001b) showed how the severity of pathogen transmission across a patch boundary could determine the persistence or extinction of local host populations.

Perhaps the most pronounced shortcoming of the various theoretical approaches to modeling dynamics involving ecological boundaries is that, except for the spatially implicit models, none of them can easily handle temporal changes in boundary conditions or feedback between the processes operating across the boundary and the changes to the boundary itself. In contrast, recent empirical research, especially studies of forest fragmentation, has made clear that boundary conditions change over time, and that this temporal dependence can manifest itself in several distinct ways (see, e.g., Hardt and Forman 1989, Cummings and Vessey 1994, Laurance et al. 1997). Because detecting changes in the location or characteristics of boundaries constitutes a major line of investigation for statisticians conducting research on boundaries, the lack of a substantial counterpart to these changes on the modeling side seriously inhibits increased integration of statistical and dynamic modeling perspectives.

Sometimes the time frame of boundary change is sufficiently long relative to the ecological processes of interest (e.g., predator–prey interactions) that the boundary can be viewed as static. At other times, however, explicit recognition of temporal changes in boundary conditions is required. For example, some forest clear-cut edges can close up relatively quickly following harvest, limiting boundary permeability to a narrow window of time for some species (Williams-Linera 1990). However, because the rate of sealing of patch boundaries depends on such variables as aspect, vegetation type, and the degree of disturbance associated with edge creation, in some cases cross-boundary propagule dispersal may remain high for years. In other cases, successional processes may diminish the hostility of boundary conditions over time as the structure of cleared areas converges on that of forest patches (Matlack 1994). In still other cases, significant lag effects exist such that edges become increasingly hostile the longer the time elapsed since clearing (Laurance et al. 1997).

A second kind of temporal dependency involves cases in which the location of the boundary changes over time. Examples include the expansion of forest boundaries through dispersal of seeds from interior trees (Hardt and Forman 1989, Laurance et al. 1997) and patch contraction caused by tree mortality at the boundary. Despite their structural differences from forest patches, similar outward and inward movements of boundaries occur in intertidal zones (Paine and Levin 1981) and sea-grass beds (Jensen and Bell 2001).

The examples above all involve edge changes that are, at least approximately, unidirectional in nature. A third, and very different, kind of temporal dependency arises when boundary structure or its influence on dispersal varies periodically according to daily (Paine and Levin 1981) through seasonal (Cummings and Vessey 1994) cycles. A key effect of such temporal forcing is to concentrate species interactions or other processes into narrow windows of time, thus inducing temporal heterogeneity in processes already operating on a spatially heterogeneous landscape.

One reason ecological PDE models have generally neglected temporal dependencies in boundary conditions is that even preliminary analytical models would require fundamental advances in the underlying basic mathematics before applied scenarios could be fully represented and explored. For example, although existing PDE theory can handle cases in which species' population densities vary periodically inside a patch, questions involving unidirectional and periodic changes in boundary structure would require new theorems relating to population persistence under time-varying boundary conditions. In contrast, the cases involving mobile boundaries would require extension of results from so-called free boundary problems, which, outside of ecology, have been used to study physical processes such as melting ice and the landward intrusion of seawater wedges in deltaic regions. Although exploration of these conceptual issues in ecological contexts using PDE models must await mathematical developments, related issues could be studied now using SEPMs and other simulation methods. The conduit and filter functions of edges (Forman 1995, Strayer et al. 2003) exemplify areas in which SEPM-based theory could provide insights.

Conclusion

As a direct consequence of greater landscape fragmentation worldwide, the growth of habitat edges has far outpaced advances in our understanding of processes associated with them. Recent studies have documented the impressive array of processes that are mediated by habitat edges, including disease transmission, speciation, and community decay induced by global warming. This complex assortment of processes, and the profound diversity of ecological boundaries themselves, requires that ecologists develop rigorous methods for detecting the location and movement of boundaries and analyzing their consequences. The statistical detection and delineation of boundaries and the dynamic modeling of habitat edges represent two promising avenues for advancing our understanding of boundary structure and function across a variety of spatiotemporal scales. However, further progress will require improved linkages between observable, boundary-related patterns and the complex processes operating across habitat boundaries. Near-term opportunities exist for uniting statistical monitoring with dynamic modeling to study the nature and consequences of boundary characteristics and positions.

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