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Chapter 2

Ecological Effects of Administrative Boundaries

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All lands, no matter how large or small, remote or near, pristine or modified, are delineated by administrative boundaries. As Forman (1995) noted, "The history of civilization is a saga of linearization or geometrization of the land. The soft curves of nature have been replaced by the hard lines of humans. What are the ecological gains and losses from this seemingly inevitable process?" Imposed for a variety of purposes, boundaries have many intentional and unintentional effects on the surrounding lands. When different land-use practices are imposed on either side of the thin line of the administrative border, a distinct ecological boundary zone is inevitably created that can filter, block, or concentrate the movement of such diverse things as animals, seeds, fire, wind, water, and nutrients. These effects isolate areas from one another, with long-term and far-reaching effects on the lands on either side of the boundary.

To understand the effects of administrative boundaries we first define borders and the boundary zone surrounding borders, discuss structural and functional attributes of boundaries, and last develop a conceptual model of the major ecological effects caused by boundaries. Although it is simple, the model provides a structured framework for understanding potential boundary effects that may be useful in planning and mitigating the adverse ecological effects of administrative boundaries. We conclude that administrative boundaries may have profound effects on ecological systems: Understanding these effects and the larger cultural and ecological context of landscapes is fundamental to improving the long-term stewardship of the natural resources that provide benefits and services valued by society.

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Administrative Boundaries

Administrative borders or boundaries are lines that separate different ownerships, jurisdictions, or responsibilities, and often different management philosophies, goals, and practices. Private property boundaries, for example, are usually clearly defined by surveys, whereas federal, state, and local governments confer jurisdiction to management agencies through acts or statutes. Boundary lines are typically placed for historical, political, economic, or social reasons, forming a complex mosaic of lands owned by different parties and used for different purposes. The Greater Yellowstone area, for example, occupies more than 7.3 million hectares and is administered by three states, two national parks, three national wildlife refuges, four federal agencies, as well as numerous private owners, all with different management goals (see Chapter 11). The administrative boundaries separating diverse private and public lands are usually well known by those who have jurisdiction over the land, as are the borders between areas designating different management actions on land owned by a single entity. The USDA Forest Service, for example, has many different management designations and goals for its land.

Administrative boundaries are often placed on the landscape without regard to natural discontinuities or transitions, such as between forest and grassland or along topographic changes. When viewed on a map, these boundaries typically exhibit the rectalinearity of political, social, and economic compromise. When viewed from the ground, borders may be marked or not, obvious or subtle. Some boundaries are marked with fences or other structures and signs denoting ownership and use. Other boundaries are not marked or obvious, such as between a designated wilderness and adjacent multiple-use forest or along the middle of a stream. An administrative border is like a glass wall that may not be readily apparent, but because nearly all terrestrial and aquatic ecosystems are open systems requiring continual flows or fluxes of energy and matter, differences in management goals and land-use practices on either side of the border inevitably disrupt these flows, causing changes in ecological conditions and processes.

Conceptual models of natural ecological boundaries, their attributes, and their effects have been developed for terrestrial systems (Wiens et al. 1985, Forman and Godron 1986, Gosz 1991, Forman and Moore 1992, Wiens 1992, and Forman 1995), and for riverine systems (Naiman et al. 1988). Schonewald-Cox and Bayless (1986) and Buechner (1987) devel-

oped boundary models for the specific case of nature reserves. Although our focus on administrative boundaries is more restrictive than the models developed generally to understand ecological boundaries and more expansive than for one specific type of administrative boundary, we do draw extensively from these substantial and important efforts in developing a conceptual model to describe administrative boundaries and their ecological effects.

Attributes of Administrative Boundaries

Administrative boundaries exhibit two general types of attributes: structural and functional. Structural attributes describe the physical aspects of a boundary and the changes that occur across or along it; functional attributes describe the flows that occur across or along a boundary. In-depth discussion and examples of boundary attributes may be found in Holland et al. (1991), Hansen and di Castri (1992), and Forman (1995); we selectively discuss those attributes and impacts that are especially relevant to administrative boundaries. Even though they are discussed separately, structural and functional attributes strongly interact with one another to determine the ecological effects caused by administrative boundaries. In addition, these attributes change over time because of natural ecological change, as management outcomes take effect or as management goals change.

Structural Attributes

Initially an administrative boundary simply is a line on a map, but over time a three-dimensional boundary structure develops that includes its width, height, and length (Figure 2.1). Width is the perpendicular distance from the administrative border that is occupied by altered habitat caused by the penetration of different ecological conditions, such as temperature, moisture, plants, animals, or seeds from one area into an adjacent area. This area of altered habitat has been called the induced or generated edge (Schonewald-Cox and Bayless 1986) because it is an artificial area produced by the different management actions on either side of the administrative border. The generated edge is similar to an ecotone where elements from distinct adjacent areas intermix. Height is the vertical profile or structure at the boundary, as well as the difference in vertical structure across the generated edge. With markedly different management actions occurring on either side of a boundary, differences

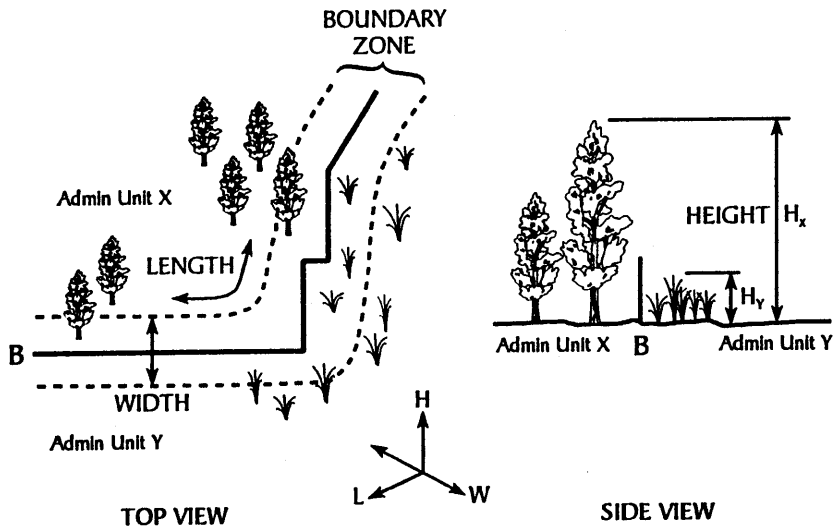

Figure 2.1. Primary structural attributes of administrative boundaries, illustrating width, height, and length attributes. The boundary zone includes the administrative border (B) between two administrative units (denoted X and Y) as well as the area influenced by the reciprocal actions of the adjacent ecological systems on each other. (Modified from Forman and Moore 1992.)

in vertical structure can be pronounced, as between clear-cut and uncut forest or between pasture and forest.

Length is the linear distance along an administrative boundary (Figure 2.1) and can be derived in several ways: actual length, straight-line length, or curvilinearity (actual divided by straight-line length). Length also can be combined with other features of a site, such as the area enclosed by the boundary, to yield insightful analyses. For example, the perimeter-to-area ratio is an important component of the filtering function of boundaries (see later). In addition, a boundary can be divided into distinct segments based on different criteria, such as patterns of ownership or vegetation types. Boundary segmentation may then be used to analyze potential impacts on different portions of a boundary or to derive a general estimate of potential impacts by examining segment variability along a boundary's length. In Organ Pipe Cactus National Monument, for example, Schonewald-Cox and Bayless (1986) analyzed boundary segments to track human-caused threats to vegetation.

Additional structural attributes include contrast and porosity. Contrast is the amount of change across the generated edge (Figure 2.2). Any variable, such as temperature or humidity, or the density of a plant or animal species, or the concentration of a soil nutrient, can vary across a gen-

erated edge, forming a gradient of change. Lower contrast presents less of a barrier to fluxes across a boundary, and discrete areas of lower contrast along a boundary may represent a "pore" allowing easier flow across a boundary. Disturbances that run perpendicular to a border, whether natural (such as a fire or a wind storm) or anthropogenic (such as a road), may create pores by obliterating the differences on adjacent sides of a border, thereby decreasing contrast. Recreational trails, for example, are small-scale disturbances that cross administrative borders and allow access to exotic plants that otherwise may not have been able to enter an area (Tyser and Worley 1992), and fires may allow exotic plants to penetrate widely across a protected area (Floyd-Hanna et al. 1993). Segmenting a boundary into categories of low, intermediate, or high contrast may yield estimates of boundary porosity, or the degree to which a given length of boundary impedes or facilitates a specific type of flow across it. Because different types of flows are impeded or facilitated by a boundary differently, boundary porosity must be clearly identified in reference to a specific type of flow.

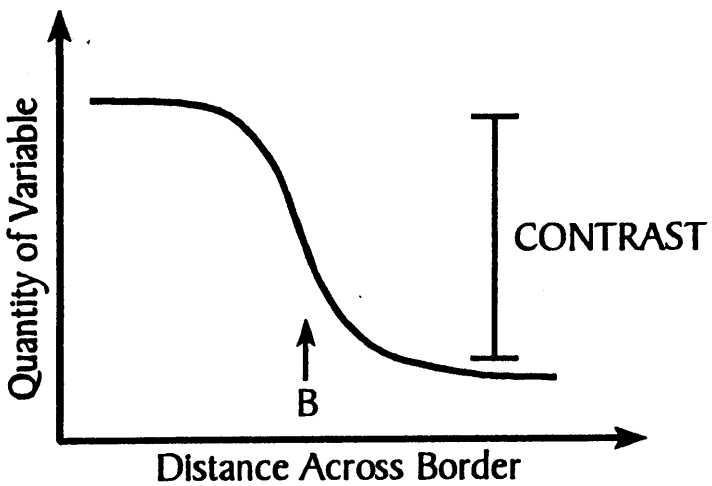

Figure 2.2. Gradient of change in any ecological variable across an administrative boundary zone. The vertical axis represents the state of any ecological variable of interest, for example population density of a particular species, concentration of a soil nutrient, ambient temperature or humidity, reproductive rate of a plant species, or predation rate on ground-nesting birds. The horizontal axis represents the distance or width across a boundary zone, and B denotes the location of the administrative border. Contrast is the amount of change in the variable of interest across the boundary zone or across a predetermined unit of distance.

The amount of change per unit distance across a boundary (Figure 2.3) can vary independently of contrast, also affecting flows across a boundary area. Areas with high contrast and a high rate of change likely pose the greatest barriers to natural fluxes across a boundary, whereas areas with lower rates of change likely pose less of a barrier to cross-boundary fluxes because the contrast per unit area is reduced. Buffer zones often are suggested for reducing the negative effects of administrative borders, and this proposed benefit may largely result from the increased width of the boundary zone, thereby reducing the rate of change and contrast across the boundary. In other instances, areas with high contrast may allow certain species access to habitats that they otherwise may not have entered. Brown-headed cowbirds (*Molothrus ater*), for example, are nest parasites that live in open fields where water is available, yet they fly up to seven kilometers into adjacent forest to lay their eggs in the nests of forest interior migratory songbirds (Rothstein et al. 1984).

Functional Attributes

There are two primary functional attributes of boundaries: a conduit function affecting flow along the length of a boundary, and a filtering function affecting flow across the boundary.

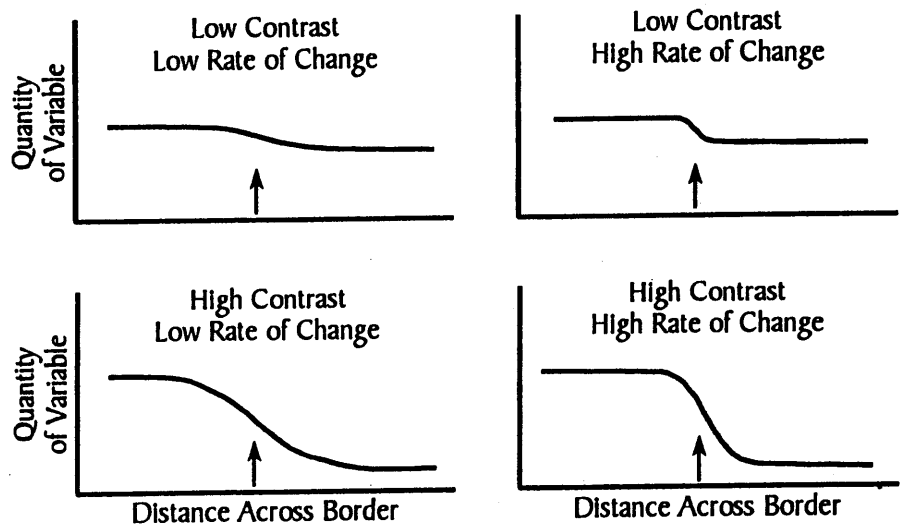

Figure 2.3. Four possible combinations in the amount of contrast and the rate of change in the variable of interest across a boundary zone. The small vertical arrow denotes the location of the administrative border.

Conduit Function

The creation of a boundary can markedly affect fluxes along this edge. Mule deer (*Odocoileus hemionus*), for example, move along certain forest edges in New Mexico (Forman and Moore 1992), shifting the population from one area to another. In human-dominated landscapes, roads often are placed close to administrative boundaries, so that vehicular or foot traffic is a common flux along the boundary, affecting many of the plants and animals in this area. Pollutants from motor vehicles also "splash" through the boundary along the road, affecting the ecosystem beyond in a linear strip along the border (Smith 1990). Convolution, or curvilinearity of the edge as seen on a map, can influence how the administrative boundary affects fluxes along it. Forman (1995), for instance, found that boundary curvilinearity affected the use and movement patterns of elk (*Cervus canadensis*) and mule deer: as curvilinearity increased, movement along the border decreased and movement across the border increased. Although administrative boundaries have been shown to affect some fluxes along them, this conduit function has received little attention from ecologists, and there is little understanding of the fluxes that are affected and of the mechanisms driving them.

Filtering Function

Flows of matter or energy occur within the ground, along the surface, and in the air (Figure 2.4). Virtually everything moves across a landscape by one of two modes (Forman 1995): locomotion (e.g., animals), or as part of the mass flow of air or water (e.g., nutrients, seeds, spores, soil, tree leaves). Because the boundary zone is different from the surrounding area, these flows may be impeded, accelerated, or not affected as they encounter this zone (Figure 2.5). Like the selective permeability of a cellular membrane the boundary thus acts like a selective filter altering flows across it. Ambrose (1987) applied this analogy in discussing the impact of the administrative boundary on Great Smokey Mountains National Park. Forman and Moore (1992) review how the thermodynamics and molecular phenomena of membranes provide "a highly informative analogy" and "a solid foundation for understanding landscape boundary structure and function."

The filtering function regulates the flow of energy and matter across a boundary, influencing not only what moves across the boundary, but also how fast and how much. Filtering is one of the most important effects of

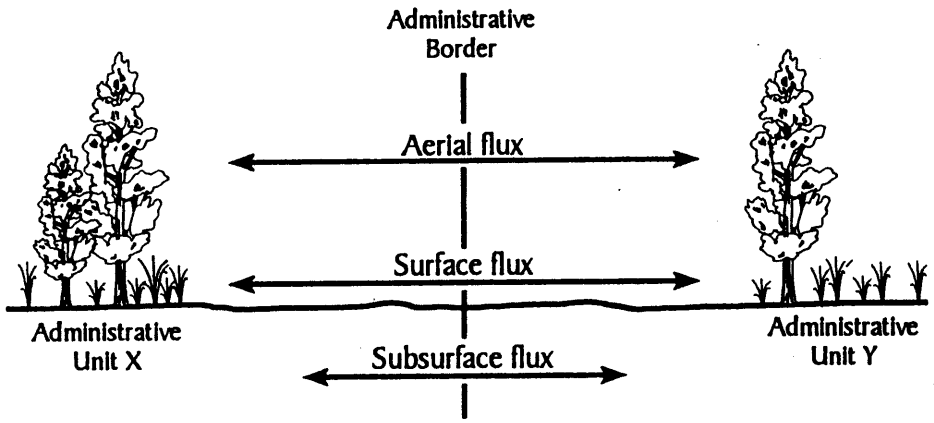

Figure 2.4. Three types of ecological fluxes affected by an administrative border and boundary zone. Aerial and surface fluxes generally move greater distances than subsurface fluxes.

boundaries, and administrative boundaries often are intentionally established to provide this filtering function. For example, during a timber-harvesting operation, water and soil nutrients are allowed to flow in while recreationists are excluded; in designated wilderness, recreationists are allowed in while motorized and mechanized vehicles are not. Unintentional ecological effects of boundary filtering are likely greater than the intentional effects and are discussed under Ecological Effects of Administrative Boundaries.

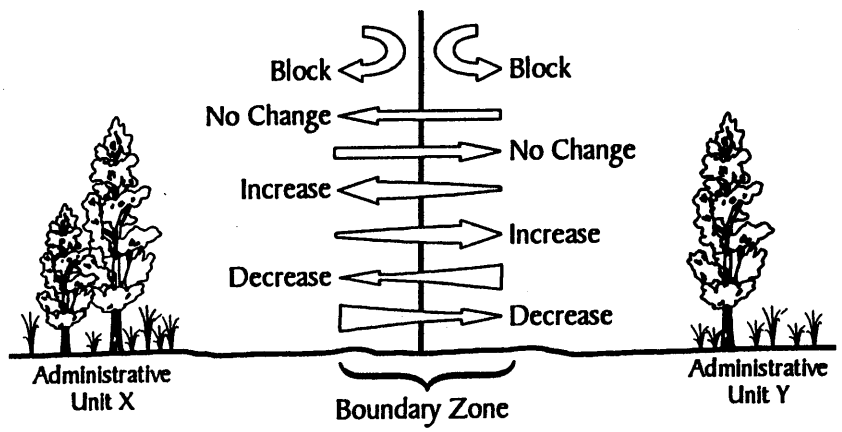

Figure 2.5. Possible changes in fluxes and flux rates across an administrative border and boundary zone. Either administrative unit may act as the "focal" side from which fluxes may increase, decrease, or not change; either side may therefore be a source or a sink for a resource, contaminant, influence, or organism. The boundary zone functions as a semipermeable membrane profoundly affecting ecological flows across a landscape.

Filtering Mechanisms

Inferences derived from natural ecological boundaries provide an organizational structure for discussing filtering mechanisms of administrative boundaries. Boundary filtering may be largely influenced by two interacting factors: the probability of encountering a boundary, and the probability of crossing a boundary (Wiens 1992). Both probabilities are strongly influenced by multiple factors, especially landform physiography, structural attributes of the boundary, and characteristics of the abiotic or biotic vector (e.g., wind or water, or animals, respectively). Landscapes with steep elevational gradients and topographic complexity exhibit greater potential energy of gravity and differential heating and cooling (causing airflow), increasing the likelihood that both types of vectors encounter and cross an administrative boundary. For example, Swanson et al. (1992) found that landform complexity strongly influenced the pattern of water movement and disturbances, thereby affecting the pattern and density of plant association ecotones. Alternatively, topographic complexity may hinder the movement of small and slow-moving animals because of the greater distances involved, as well as the different microclimates and other factors found in complex terrain.

Perimeter-to-area ratio is an important structural attribute of administrative boundaries that influences filtering. A large perimeter-to-area ratio indicates that most vectors, whether abiotic or biotic, have a higher probability of encountering the boundary. For example, Stamps et al. (1987) found that insect emigration and immigration rates were higher in areas with higher perimeter-to-area ratios, and Buechner (1987), using simulation models, found that patch perimeter-to-area ratio was the major factor influencing animal movement across patch edges.

Several characteristics of biotic vectors, including mobility, size, demographics, and behavior, also influence the likelihood of encountering and crossing an administrative boundary. Great mobility, whether because of flight (e.g., bats, insects, and birds), small size that allows individuals to be carried by wind or water across land (e.g., spores, or small seeds), or large size that allows individuals to travel large distances (e.g., large ungulates and large predators), increases the chances of encountering and crossing a boundary. Large size also confers physiological buffering against changes in external conditions, allowing large animals to cross high-contrast areas where there may be large differences in ecological conditions. A large population density in one area may force individuals to disperse into adjacent areas, increasing the likelihood of con-

tact with a boundary. Alternatively, high population densities in an adjoining area may create a "social fence" that prevents dispersal into that area, as Hestbeck (1982) hypothesized for certain rodents. The habitat-selection preferences and behaviors of species also can strongly influence the probability of boundary crossing.

Boundary filtering is influenced by the probabilities of a vector encountering and crossing a boundary. The likelihood of any vector crossing a boundary is highest when both probabilities are high. Conversely, when both probabilities are low, it is not likely that a vector will cross a boundary. When one probability is low and the other is high, the outcome of boundary filtering is uncertain. For example, although a single low-contrast segment may allow most abiotic and biotic vectors to cross a border easily, if the vector never encounters this segment, no boundary crossing will occur. By contrast, large-scale disturbances, such as wind storms or fire, are more likely to decrease contrast over a greater length of administrative border, allowing cross-boundary movement of abiotic and biotic vectors over this larger area. Boundary filtering is therefore a vector-specific and context-specific process.

Ecological Effects of Administrative Boundaries

An administrative boundary has no ecological effect when first established as merely a line drawn on a map. Shortly thereafter, different goals for the land on either side of the boundary drive different management and land-use actions, often creating ecological differences on either side of the boundary (Figure 2.6). These ecological differences, especially in microclimate, soil, plants, and animals, establish most of the structural and functional attributes of the boundary (Forman 1995), in turn augmenting the ecological differences in a positive feedback cycle. This conceptual model of the development of boundary effects stresses that (1) management goals and actions are the primary cause of boundary effects; (2) altered flows either into or out of an area will likely be detrimental to that area; (3) boundary effects follow a distinct temporal sequence; and (4) once established, these effects may have long-term and far-reaching consequences that are difficult or impossible to overcome. Administrative boundaries fragment ecological systems in diverse ways with diverse consequences (review in Saunders et al. 1991; see also Angelstam 1992). We organize these many boundary effects into two broad groups: boundary habitat and isolation impacts.

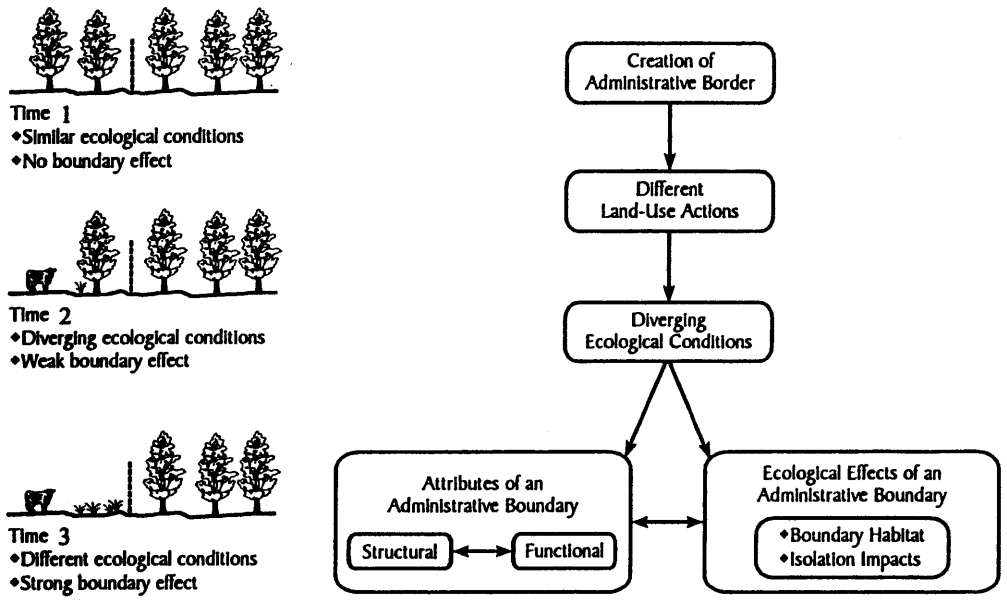

Figure 2.6. Right: Conceptual model of the development of ecological impacts caused by administrative borders. The boxes represent fairly discrete stages in the development of ecological impacts. Different land-use goals and actions on either side of the border cause ecological conditions on either side of the border to diverge. Diverging ecological conditions simultaneously both create the structural and functional attributes of the boundary zone, and cause immediate boundary habitat and isolation impacts. Structural and functional boundary attributes amplify the boundary habitat and isolation impacts, and these ecological impacts reinforce the boundary attributes in a positive feedback cycle. Left: Temporal sequence of the development of ecological impacts caused by administrative borders, corresponding to the stages of the conceptual model. Initially there is no ecological effect of the administrative border because it is simply a line drawn on a map and there are no land-use differences on either side of the border. At time 2 differences in land-use goals and actions begin to create different ecological conditions and to establish the structural and functional attributes of the boundary. At time 3 there is a strong boundary effect with self-perpetuating feedback between boundary attributes and ecological impacts.

Boundary Habitat

Boundary habitat is the distinct area or zone and set of ecological conditions surrounding an administrative border created by the reciprocal influence of the ecological systems on either side of that border. This distinct ecological boundary zone thus overlaps with and extends beyond the administrative border. Boundary habitat generally differs from the adjoining interior area in three major respects: microclimate, soil condi-

tions, and species composition (Forman 1995). Microclimatic differences in temperature and humidity occur because differing vegetation structures alter solar gain and flux. For example, light, soil moisture, humidity, and wind momentum all varied across the boundary zone from a clear-cut to an old-growth Douglas fir (*Pseudotsuga menziesii*) forest (Chen et al. 1995; see also Matlack 1993). Similar microclimate and soil effects were observed across boundary edges in tropical forests (Williams-Linera 1990, Camargo and Kapos 1995). Numerous examples of microclimate and soil gradients across boundary zones are discussed by Forman (1995).

The boundary zone may be used more intensively or heighten change in ecological fluxes. When administrative boundaries abut heavily used transportation corridors or densely settled land-use areas, they may be exposed to increased pollution loading, runoff, vandalism and human disturbance, or entry by organisms such as domestic animals, pests, or exotic plant species. Likewise, when administrative boundaries coincide with abrupt structural changes in a landscape, as between a closed canopy forest and a meadow, flux rates of important ecological materials may change. For example, Weathers and Cadenasso (1996) found that atmospheric deposition of sulfate, calcium, and nitrate, and subsequent nutrient input to the forest floor, were all higher in forest edges than in forest interiors. Higher flux rates also are driven by broad-scale patterns of land use; the greatest change in landscape heterogeneity, including patch size and density, occurs closest to the border of Great Smokey Mountain National Park (Ambrose and Bratton 1990). Therefore, boundary habitat may be a site of intensification of ecological fluxes in landscapes.

Differences in species composition between interior areas and boundary habitat have long been observed. The boundary area may have different species because of different land-use practices, microclimate and soil conditions, or a mix of species from areas adjacent to the border. Vegetation gradients across boundaries have been documented in many different ecosystems (e.g., Ranney et al. 1981, de Casenave et al. 1995, Murcia 1995, Jose et al. 1996). Management practices on one side of a border that disturb soil increase the chance that exotic plants may grow there. These plants may then invade other portions within the boundary area or beyond (Murcia 1995). By contrast, Brothers and Spingarn (1992) found that the wall of forest vegetation at the edge of a clearing effectively repelled most exotic plants, pointing to the need for more research and understanding about the movement of biotic vectors across a boundary zone.

Animals, often habitat generalists that thrive at the interface of different plant communities or seral stages, readily colonize and establish new populations in the boundary zone. Bird communities along City of Boulder Open Space borders, for example, are substantially different from those in core areas in the open space lands (Bock et al. in press). Bird communities along these open space borders are dominated by the American robin (*Turdus migratorius*), house sparrow (*Passer domesticus*), and common grackle (*Quiscalus quiscula*). Away from these borders the bird communities include species that are often less common, such as pygmy nuthatches (*Sitta pygmaea*), western tanagers (*Piranga ludoviciana*), and solitary vireos (*Vireo solitarius*).

Altered species composition in the boundary area also results from management actions on one side of a border that create favorable conditions for species that are aggressive competitors, predators, or parasites. These species then move into adjoining boundary areas or beyond, typically reducing the density of existing native species. European starlings (*Sturnus vulgaris*), for example, are highly aggressive nest competitors that displace native species both in boundary and interior areas (Weitzel 1988, Kerpez and Smith 1990). As discussed, parasitic brown-headed cowbirds invade nests in nearby forested areas. In general, the rates of nest predation among forest birds are much higher closer to borders with open land. Andren and Angelstam (1988), for example, found that predation rates were significantly higher on artificial nests within 50 meters of forest edge.

Isolation Impacts

A variety of impacts may occur far from the generated edge, primarily caused by the altered flux of species, seeds or other propagules, and disturbance processes across the boundary area. Collectively these may be called isolation impacts because the effects do not occur within the boundary area itself but within the interior of the administrative unit. Three general types of isolation impacts are particularly relevant to the administrative borders: impacts on interior or core areas, impacts on ecological processes, and impacts on populations.

Impacts on Interior or Core Areas

Away from the generated edge, habitat conditions in the interior of an administrative unit, or core area, can still be affected by conditions in the

boundary area. First, the overall size of the interior or core area is reduced with consequent impacts on populations (see Impacts on Populations). The extent to which the core area is reduced depends on many factors, principally the vegetation structure that buffers temperature and moisture conditions and the flux of abiotic and biotic vectors. A wide range of reduction in core area is reported in the literature, varying from one or two meters, to tens or hundreds of meters from the border (Forman 1995). Second, if large-scale flows are altered (see Impacts on Ecological Processes), vegetation in core areas may be drastically altered. For example, Habeck (1985) found that fire suppression on lands adjacent to the Selway-Bitterroot Wilderness increased fuel loads and the probability of fires spreading into remote parts of the wilderness and burning western red cedar (*Thuja plicata*) forests that typically burn infrequently. Third, impacts from wide-ranging exotic species can significantly alter interior areas far from administrative borders. Feral pigs, for example, have had a devastating impact on native vegetation throughout Hawaiian national parks (Stone and Loope 1987).

Impacts on Ecological Processes

Adjacent land practices and boundaries may block or disrupt vital ecological flows across large portions of a landscape. For example, irrigation diversions and power generation outside Everglades National Park and Grand Canyon National Park, respectively, altered hydrological flow regimes within these parks, severely altering vegetation and wildlife communities (Kushlan 1987, Stevens et al. 1995). In contrast to disrupted fluxes, different management goals on one side of the border may promote or enhance the spread of certain ecological flows that are detrimental to the other side of the border. Fire management illustrates the problems of both disrupted and enhanced fluxes across borders. In the first case, fires that initiated in lower elevation areas and subsequently spread up into higher vegetation types are now largely suppressed, thereby also stopping the fires that would naturally have burned up into higher elevations (Kilgore and Heinselman 1990). In the second case, the example of the Selway-Bitterroot Wilderness shows how different management actions on one side of a border result in fires spreading into areas that they typically would not reach. These changes in fire regimes extend far beyond the administrative border and most likely affect these ecosystems well into the future.

Natural ecological succession results in changes in species composi-

tion, the architecture of ecological systems, and system function over time. Nearly all ecological systems change over time, because of internal interactions or as responses to changes in the larger physical environment. Exotic species common in adjacent lands and boundary areas can fundamentally alter the course of ecological succession, causing different species composition and altered ecological functions. For example, successional pathways following a hot fire were significantly altered by the exotic musk thistle (*Carduus macrocephalus*) in Mesa Verde National Park (Floyd-Hanna et al. 1993).

Impacts on Populations

Administrative boundaries affect populations in several ways, especially by disrupting dispersal, decreasing the overall size of an area, and surrounding the isolated area with conditions and threats that are detrimental to survival. Plant and animal populations often consist of spatially separate subpopulations connected through movement from one population to another, forming a metapopulation. Dispersal is key to maintaining recruitment among the subpopulations of a metapopulation, and boundaries and intervening areas that disrupt this flow of individuals across the landscape isolate subpopulations, reduce metapopulation viability, and increase the probability of extinction. In many cases, dispersal and recolonization among fragmented populations is critical for regional survival of a species (Fahrig and Merriam 1994).

An isolated area is a fragment of a former larger area and may now be a "sink" area that loses individuals from a population as they emigrate from the area (Pulliam and Danielson 1991), an effect recognized long ago by Wright et al. (1933) for wildlife in national parks. For species that occupy large home ranges and disperse widely, such as top trophic level carnivores and omnivores like the grizzly bear (*Ursus arctos horribilis*) or wolverine (*Gulo luscus*), these impacts may be especially acute (Newmark 1985). In Algonquin Provincial Park, Ontario, Canada, a yearly average of 11 percent of the Park gray wolf (*Canis lupus*) population was killed by humans from 1988 through 1993 when the wolves left the Park (Forbes and Theberge 1996). Similarly, for large herbivores such as elk that migrate seasonally, boundary areas and adjacent land activities may prevent the seasonal migrations necessary for survival (Lyon and Ward 1982). Bison (*Bison bison*) leaving Yellowstone National Park are killed because they may be vectors for brucellosis, a disease causing higher abortion rates in livestock (Meagher 1989, Keiter 1997).

Isolated populations are more susceptible to extirpation from many causes (reviewed by Lande 1993), including disease, predation, competition, disturbances. Isolated populations also suffer a variety of genetic problems associated with a smaller effective population size, including reduced heterozygosity, inbreeding depression, and genetic drift (reviewed by Brussard and Gilpin 1989). For example, reduced fertility in fewer than fifty remaining Florida panthers (*Felis concolor coryi*) caused by inbreeding depression now contributes to an even smaller population size (Ballou et al. 1989). Dispersal among relatively isolated subpopulations is essential to maintaining species' genetic integrity and variability, but boundary habitats may restrict or prevent dispersal. Based on genetic theory, the notion that one individual per generation moving into a population could maintain the population's genetic integrity has been applied as a rule of thumb in designing conservation programs for many different species. Mills and Allendorf (1996) reviewed these uses and the assumptions behind this rule of thumb, concluding that for genetic purposes only this rule provides an adequate minimum floor for immigration rates.

Both boundary habitat and isolation impacts may persist long after the boundary has served its intended purpose. The species composition on two sides of a tumbledown fence that once separated a pasture from a row crop field is one example; an ancient Anasazi village boundary in the Colorado Plateau is another. The use and ecological significance of such contrasting patches may differ because of contrasting nutrient concentrations or vegetation composition and structure that have persisted into the present. Therefore, how these contrasting patches are used now may well depend on what people did there long ago. Altered species composition and ecological processes, such as fire and succession, also may fundamentally change the ecological system, moving it to a new ecological state (Sprugel 1991).

Research Needs

Current understanding of administrative boundaries and their ecological effects is insufficient for effective landscape-scale stewardship. Compounding the problems of meager understanding, there is little or no strategic planning to integrate research on multiple causal factors. For example, data do exist on plant and animal species composition across boundaries, but most other factors contributing to the structure of the boundary zone have been neglected. In cases where the physical envi-

ronment has been measured, those measurements have neglected soil processes and structures or have been taken independently of detailed quantification of the vegetation gradients across edges. In this section we offer an agenda for boundary-related research, focusing on four topics: boundary structures, fluxes and gradients along and across these structures, filtering mechanisms affecting fluxes across boundaries, and the ecological effects within and beyond the boundary zone.

Boundary Structures

To understand the ecological implications of different administrative borders, one of the first research priorities is to develop better knowledge about the three-dimensional ecological structure of the boundary zone. What are these structures? Where do they occur? How do they develop? How do they influence the boundary zone? Ultimately, the purpose of describing the three-dimensional structure of a boundary is to relate this structure to important ecological functions or management goals. To date, however, relatively few of the structures that contribute to boundaries have been quantified and described, either along the length of a boundary or how these structures change over time due to natural succession or other changes brought about by land-use decisions. For example, the conditions that contribute to contrast, porosity, boundary segmentation and segment variability are known basically from conceptual models that have received little confirmation from empirical studies. Even though geographic information systems based on remotely sensed data offer much promise for detecting and quantifying landscape-level boundaries (Johnston et al. 1992) and administrative borders, techniques for delineating natural ecological boundaries are still in their relative infancy (McCoy et al. 1986, Fortin and Drapeau 1995). Because the administrative boundary zone also is an ecological boundary, a better understanding of natural ecological boundary structures and fluxes across them may greatly improve how we understand and manage administrative boundaries.

Fluxes and Gradients

One of the most significant impacts of administrative boundaries is how they alter ecological fluxes across a landscape. What are these abiotic and biotic fluxes? How did they move across the landscape before the border was in place? How do they move across the landscape now? What

are the effects of these altered fluxes on the valued attributes that occur on both sides of the boundary? How do these fluxes change over time and along the length of a boundary? Most studies have focused on the static state of a variable at fixed points across the boundary. It is also important to begin measuring actual fluxes of materials and energy across boundaries, especially the movement and behavior of nutrients, organisms, and disturbance processes. For instance, the movement of exotic seeds through the boundary zone and into the interior needs to be quantified so that the potential impact and strategies for managing these species can be determined. The movement patterns and behavioral responses of animals, especially insects, birds, and predatory and herbivorous mammals, must be better understood to manage and restore fragmented forests in today's cultural landscapes.

Research also can describe the many ecological gradients and trends across boundary zones, ranging from plant and animal population densities, vegetation architecture and microclimate, and soil nutrient and organic matter concentrations, to rates of soil nutrient turnover, primary productivity, and decomposition. Quantifying gradients across boundaries requires an arbitrary starting or zero point through which the gradients run. However, the specific location of this arbitrary point is rarely stated. Furthermore, researchers may assume that this point defines one end of the gradient of factors that change across the boundary, but these gradients can extend well beyond the usual structural anchors. For example, changes in environmental factors to levels characteristic of the forest can actually occur outside the wall of understory vegetation defining the structural edge of the forest (Cadenasso et al. 1997). Researchers need to examine entire ranges of environmental gradients at boundaries, and not assume that a structural anchor is necessarily the ecological end point of the gradient.

Filtering Mechanisms

Although it is well known that boundaries act as semipermeable membranes blocking, increasing, or decreasing flows into and out of areas on either side of the border, there is little understanding of filtering mechanisms. How do boundary structures, such as width, contrast, segmentation, or convolution, affect flows? Which flows are affected, and how much are they affected? What are the temporal dynamics of filtering? For instance, are some flows affected only during some seasons? What are the spatial dynamics of filtering? For instance, are some flows affected only in

some places? What are the primary drivers influencing the probability of different abiotic and biotic vectors encountering and crossing a boundary area? There is a plethora of questions related to filtering mechanisms. The answers will provide the grist for improving both basic knowledge about natural ecological boundaries and management frameworks for reducing the ecological impacts of administrative boundaries.

Ecological Effects

As with filtering mechanisms, the research needs for understanding the ecological effects of administrative boundaries are vast. Three basic questions can help structure this discussion of research needs: What are the short-term, small spatial-scale effects? What are the long-term, large spatial-scale effects? And, what are the cumulative effects of multiple factors?

Short-term effects are the changes within the boundary area resulting from different management and land-use actions on either side of the border, as well as changes in fluxes across the boundary. What components, such as species or vegetation types, are affected? Do certain boundary attributes have a greater or lesser effect on certain components? Substantial information on game species in ecotones provides some answers, but short-term effects on other species and on most processes, and on the mechanisms of these impacts, are largely unknown.

Long-term, large-area effects are poorly understood, yet these effects may have the greatest impact on the long-term productivity of ecological systems, including those systems that produce goods and services valued by society. Important research questions abound. How does the boundary area, as well as the structural and functional attributes of boundaries, change over time? Will a different species milieu in boundary and interior areas alter successional pathways and lead to entirely different ecosystems? How far away from a boundary will species composition, population demographics, and ecological flows be affected? How long will these effects persist? Administrative boundaries and adjacent interior areas provide an opportunity, and reason, to test basic ecological concepts on community invasibility, resilience, and multiple stable states.

Ecological impacts from administrative boundaries come in suites, not singly as described in this chapter. For example, a boundary would simultaneously affect a population in several ways: disrupted dispersal of individuals; exposure to new biotic vectors such as exotic species; exposure

to new microclimatic conditions; altered flow of disturbance processes such as fire; and reduction in the genetic integrity of the population due to isolation effects. These impacts have both short- and long-term consequences. In addition, they most likely are synergistic, resulting in even greater impacts. Cumulative effects from multiple factors form the milieu of boundary impacts, but research tends to look at isolated factors, thereby improving the likelihood of successful research, but at the cost of ecological reality and management applicability. Although certainly difficult, research on multiple factors and cumulative effects would help fill the current information vacuum on methods for ameliorating boundary impacts and improving ecological stewardship across boundaries.

Conclusions

Administrative borders are not simply lines on maps. They have profound effects on the ecological systems immediately surrounding the border and far from it and may change these ecological systems in fundamental, long-lasting ways. Some of these changes are intentional, but most are not. The conceptual model of boundaries and of their effects developed here has far-reaching implications for policy, planning, and management to improve landscape-level stewardship.

First, landowners and managers need to recognize and accept responsibility for the ecological effects of their boundaries, direct and indirect, short-term and long-term, rather than treating the boundary area as an expendable commons.

Second, the boundary model developed here suggests that incongruent management goals and actions on either side of the boundary are more important in causing the disruption of ecological fluxes across administrative borders than the usually reported incongruency between administrative and ecological borders. For example, even if administrative and ecological boundaries coincided perfectly, different management goals on either side of the boundary would still cause boundary effects, including isolation impacts to the interior of the administrative units. If this supposition is correct, then in addition to striving for ecologically placed boundaries (see Theberge 1989 for guidelines), more effort is needed to make management goals and actions compatible across administrative borders. In some cases it is possible to conform management with natural ecological boundaries, such as the use of ridge lines or rock outcrops as natural fire breaks by fire manage-

ment officers in defining fire management zones. Even though most administrative borders are fixed, such as borders between agencies, borders defining management zones *within* an agency have a much better chance of conforming with ecological boundaries. Therefore, reducing ecological impacts will likely require two approaches: striving to make management goals and actions compatible across administrative borders, and making internal management borders and ecological boundaries coincide.

Third, buffer zones may alleviate some, but not all, of the ecological impacts caused by administrative boundaries. By reducing the contrast or the rate of change between adjacent areas, buffer zones may permit more natural ecological flows across a boundary. However, creating buffer zones also increases the width of the generated edge, potentially exacerbating or causing additional ecological impacts. In general, the greater the difference in management goals on either side of a border, the greater the need for, and width of, a buffer zone. Clear-cutting up to the edge of a wilderness, for example, has the greatest ecological impact; a buffer zone within the timber management area would temper some of these impacts.

Finally, landscape-scale stewardship requires landscape-scale planning and management. A management style that focuses solely on particular isolated parcels of land is likely to fail to produce desired long-term outcomes because the health and productivity of all ecosystems are contingent on the larger cultural and ecological landscape of which they are a part (Pickett and Ostfeld 1995). Even interior or core areas are embedded in a larger environmental context and are affected by management goals and actions on surrounding lands. Petit et al. (1995) offer a detailed example of landscape-level planning and management for neotropical birds. The information in this chapter strongly points to the critical need for explicitly taking into account the ecological effects of administrative boundaries and for developing a landscape-scale perspective that takes into consideration larger areas and longer time frames, and fosters coordinated planning and setting of land-use goals.

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