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ECOLOGICAL MECHANISMS LINKING PROTECTED AREAS TO SURROUNDING LANDS

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Abstract. Land use is expanding and intensifying in the unprotected lands surrounding many of the world's protected areas. The influence of this land use change on ecological processes is poorly understood. The goal of this paper is to draw on ecological theory to provide a synthetic framework for understanding how land use change around protected areas may alter ecological processes and biodiversity within protected areas and to provide a basis for identifying scientifically based management alternatives. We first present a conceptual model of protected areas embedded within larger ecosystems that often include surrounding human land use. Drawing on case studies in this Invited Feature, we then explore a comprehensive set of ecological mechanisms by which land use on surrounding lands may influence ecological processes and biodiversity within reserves. These mechanisms involve changes in ecosystem size, with implications for minimum dynamic area, species–area effect, and trophic structure; altered flows of materials and disturbances into and out of reserves; effects on crucial habitats for seasonal and migration movements and population source/sink dynamics; and exposure to humans through hunting, poaching, exotics species, and disease. These ecological mechanisms provide a basis for assessing the vulnerability of protected areas to land use. They also suggest criteria for designing regional management to sustain protected areas in the context of surrounding human land use. These design criteria include maximizing the area of functional habitats, identifying and maintaining ecological process zones, maintaining key migration and source habitats, and managing human proximity and edge effects.

Key words: ecological processes; ecosystem size; edge effects; habitat; land use change; management; protected areas; vulnerability.

Introduction

Human societies have long set aside tracts of land to conserve nature in the form of hunting reserves, religious forests, and common grounds (Chandrashekara and Sankar 1998). The current concept of national parks evolved in the mid 1800s as European colonists were converting native landscapes to farms, ranches, and cities (Schullery 1997). A key goal was the protection of nature. By minimizing the influence of humans, natural ecosystems were expected to continue to maintain ecological processes and native species.

During the 20th century, protected areas became a cornerstone of the global conservation strategy. New protected areas continue to be established: the total number globally has doubled since 1975 (Ervin 2003*a*). The term "protected area" refers to any area of land or sea managed for the persistence of biodiversity and other natural processes in situ, through constraints on incompatible land uses (Possingham et al. 2006). The basic role of protected areas is to separate elements of biodiversity from processes that threaten their existence in the wild (Margules and Pressey 2000). Recent assessments have found that most terrestrial reserves are adequately protected within their borders (Bruner et al. 2001, DeFries et al. 2005).

Despite the high level of protection afforded national parks and other protected areas, many are not functioning as originally envisioned. Critical ecological processes such as fire, flooding, and climate regimes have been altered (Lawton et al. 2001, Pringle 2001). Exotic species are increasingly invading protected areas (Stohlgren 1998), and some native species have gone extinct in protected areas (Newmark 1987, 1995, 1996, Rivard et al. 2000, Brashares et al. 2001). For example, 11 of 13 national parks in the western United States have lost large mammal species since park establishment, with 5–21.4% of original species lost (Parks and Harcourt 2002).

Why are many protected areas not functioning well, despite adequate management within their borders? A major reason may be that human land use is expanding

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and intensifying on the lands surrounding protected areas, resulting in changes in ecological function and biodiversity within protected areas.

Recent satellite-based change analyses are revealing that human populations and intense land use have grown rapidly in recent decades around many protected areas (Hansen et al. 2004). In the tropics, road construction, conversion for agriculture, and demand for natural resources are leading to clearing of primary forest around reserves (Mustard et al. 2004) and increased hunting of native species (Escamilla et al. 2000). DeFries et al. (2005) found that 66% of 198 reserves in the humid tropics had undergone loss of forest habitat in the surrounding lands since 1980, with an average loss rate of 5% per decade within 50 km of the boundary. In other areas, increases in wealth, technology, and population density are leading to more rural settlement in previously wild areas. In the United States since 1950, for example, rural residential development was the fastest growing land use type and now covers 25% of the lower 48 states (Brown et al. 2005). Some protected areas are magnets for such rural development (Chown et al. 2003). The counties around the Yellowstone National Park, for example, are among the fastest growing in the United States (Rasker and Hansen 2000). Even in long-established societies such as in China, agricultural and urban land uses continue to push into unprotected wildlands around protected areas (Viña et al. 2007).

In recent decades, ecologists have come to realize that human impacts on surrounding lands may cross the boundaries into protected areas (Buechner 1987, Dasmann 1988, Schonewald-Cox 1988). The creation of buffer zones around protected areas was recommended to minimize negative boundary influences (Noss 1983). Accordingly, UNESCO's Man and the Biosphere (MAB) program advocated managing the lands around protected areas along a gradient of decreasingly intense land use toward protected area boundaries (UNESCO 1974). More recently, methods have been developed to evaluate the effectiveness of protected areas, with consideration of human activities on surrounding lands (Hockings 2000, TNC 2000, Ervin 2003*b*). For some protected areas that are not functioning adequately, "systematic conservation planning" (Margules and Pressey 2000) has been used to guide management of the regions around protected areas to better achieve conservation objectives (e.g., Pressey et al. 2003).

Such efforts to mitigate boundary influences on protected areas will be most effective if based on scientific understanding of the underlying ecological mechanisms. It can be difficult to ascertain the means by which human activities outside of protected areas, sometimes tens to hundreds of kilometers away, can impact ecological function and biodiversity within protected areas. Knowledge of these ecological connections could help to answer several management-oriented questions. How large is the zone of influence around a protected area? Are all locations within this zone of influence equally important to protected area functioning? Which ecological processes or species of organisms within protected areas are particularly sensitive to surrounding land use? Which land use types and intensities are most likely to have negative impacts within protected areas?

Advances in spatial ecology have allowed an increasing understanding of the ecological mechanisms connecting protected areas to surrounding lands. Island biogeography theory, for example, provides a basis for predicting extinction rates of species as a function of habitat fragmentation (Brooks et al. 1999). This theory can be applied to address the effects of habitat loss outside of protected areas on species richness within protected areas (DeFries et al. 2005). Metapopulation theory provides a basis for determining whether a subpopulation of a species within a protected area is dependent upon population source areas located in surrounding lands (Sinclair 1998, Hansen and Rotella 2002). The purpose of this paper is to draw from diverse studies of spatial ecology to derive a comprehensive overview of the ecological mechanisms by which land use outside of protected areas may influence ecology and biodiversity with protected areas. This synthesis is meant to enhance the theoretical underpinning of efforts to assess the effectiveness of protected areas (e.g., Parrish et al. 2003) and systematic conservation planning across regions including protected areas (Margules and Pressey 2000).

Our central thesis is that protected areas are often parts of larger ecosystems and that land use change in the unprotected portion of the ecosystem may rescale the ecosystem, leading to changes in the functioning and biodiversity within the reserve. We first present a conceptual model of protected areas embedded within larger ecosystems that often include surrounding human land use. We then explore the key ecological mechanisms by which this land use on surrounding lands may influence ecological processes and biodiversity within reserves. These mechanisms involve ecosystem size, ecological process zones, crucial habitats, and exposure to humans. A concluding section suggests how these ecological mechanisms provide a basis for assessing the effectiveness of protected areas and systematic conservation planning across protected areas and surrounding lands.

The case studies in the papers that follow provide more detailed examples of ways in which land use can influence protected areas. The management implications of these interactions are developed further in DeFries et al. (2007).

Protected Areas as Parts of Larger Ecosystems

Protected areas sometimes exclude a portion of the area that is needed to maintain essential ecological processes and organisms. This was recognized by scientists studying large mammals with large home ranges that

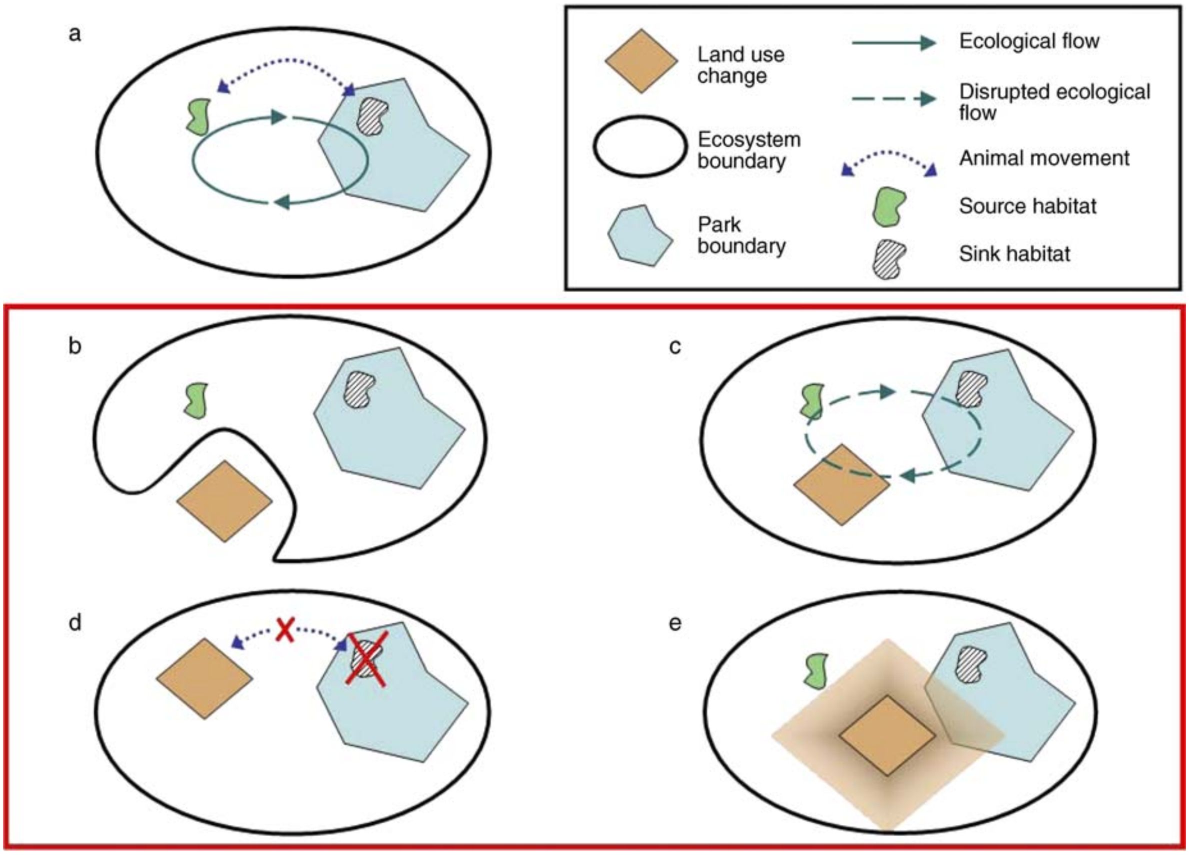

FIG. 1. Conceptual model illustrating the effects of land use change on ecosystem function. (a) Protected areas as part of a larger ecosystem with energy, materials, and/or organisms flowing through the ecosystem. (b) Land use change reduces effective size of the ecosystem. (c) Land use change alters ecological flows. (d) Land use change eliminates unique habitats and disrupts source–sink dynamics. (e) Edge effects from land use negatively influence the park.

extended outside national parks (Wright and Thompson 1935, Craighead 1979, Newmark 1985). More recently, ecologists have established that the spatial domains of ecological processes such as natural disturbance and nutrient cycling may extent outside park boundaries (Grumbine 1990). Because protected areas were often designated based on factors other than ecological completeness, such as scenic value (Pressey 1994, Scott et al. 2001), they sometimes do not include the areas required to maintain disturbance regimes, nutrient flows, organism movements, and population processes within them (Fig. 1a). Following establishment, protected areas may continue to function as parts of larger ecosystems because surrounding lands remain undeveloped and continue to provide functional habitats. If land use change reduces habitats in the unprotected portion of the ecosystem, ecosystem function and biodiversity may be degraded within the protected area. The modern concept of ecosystem management grew from the goal of managing regional landscapes to maintain the ecological integrity of the protected areas that they contain (Agee and Johnson 1988, Grumbine 1994).

How can the spatial dimensions of the effective ecosystem encompassing a protected area be quantified? If the goal of the protected area is to maintain native species and the ecological processes that they require, then the spatial extent of the effective ecosystem includes the area that strongly influences these species and processes (Grumbine 1990). This area can be mapped based on the flows of materials, energy, and organisms. Watershed boundaries are often used to define the extent of aquatic ecosystems (Pringle 2001). Watersheds encompass the area of movement of ground and surface water. Water carries nutrients such as nitrogen and phosphorous, which are critical to plant and animal growth. Water also serves as a conduit for the movements of many aquatic and terrestrial organisms. Hence, strong interactions among many components of an ecosystem may occur within watersheds. Natural disturbances such as wildfire move across landscapes from initiation zones to run-out zones and differentially influence soils, vegetation, and animal habitats within these zones (Baker 1992). Ecosystem boundaries can be delineated based on homogeneity of disturbance regimes (Pickett and Thompson 1978). Similarly, many organ-

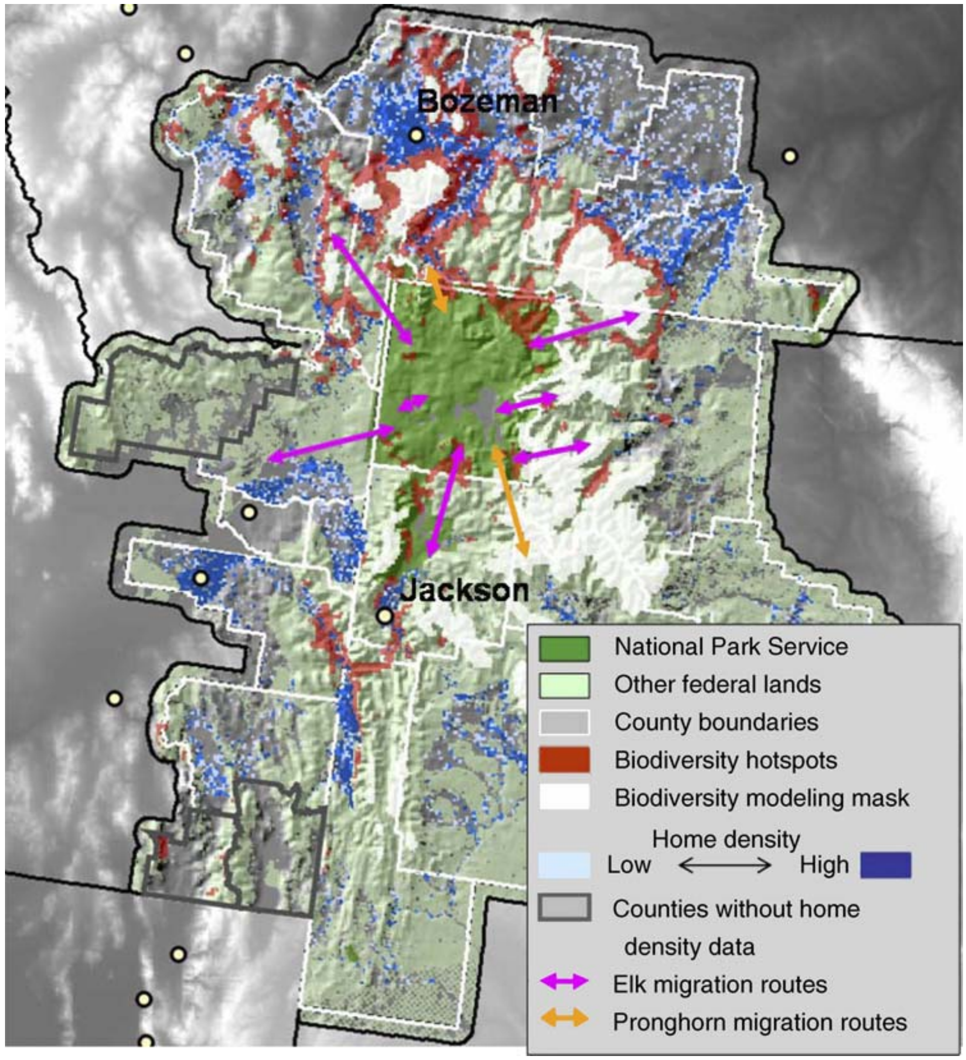

FIG. 2. Depiction of the Greater Yellowstone Ecosystem as defined based on the biophysical gradients, natural disturbance regimes, and organism movements (modified from Hansen et al. [2002] and Gude et al. [2006]). Shown are land allocation, movement pathways for two migratory species, areas of high predicted bird diversity (biodiversity hotspots), and exurban development (rural homes). The biodiversity modeling mask refers to locations too high in elevation to be within the domain of the bird diversity predictions.

isms move predictably across the landscape, for example, to gain access to seasonal resources. Ecosystem boundaries can be defined based on these movements or on the area required to maintain particular population levels of these organisms (Newmark 1985).

In practice, defining the actual boundaries of an ecosystem is subjective. Although the flows of water, nutrients, disturbance, and organisms are often interrelated, their spatial dimensions are often not identical. Water and nutrients may be well represented within watershed boundaries, but organisms may migrate among watersheds. Hence, it is often difficult to define a particular ecosystem boundary that is adequate for all components of the ecosystem. Also, the strength of interaction must be considered when defining an ecosystem. Ecological processes and organisms in a particular location are often strongly linked to some places, weakly linked to other places, and not linked to still other places. For example, climate in the Caribbean is heavily influenced by regional factors and is weakly linked to Saharan Africa via input of wind-borne loess (Prospero and Lamb 2003). Thus ecosystem boundaries are necessarily abstractions that reflect the human choice of the ecosystem property of focus and the strength of interactions used in the definition.

In a growing number of examples, protected-area-centered ecosystems have been defined (see Meffe et al. 2004). For example, the Greater Serengeti Ecosystem has been defined based on the migratory patterns of the dominant herbivore, the wildebeest (Sinclair 1995; see

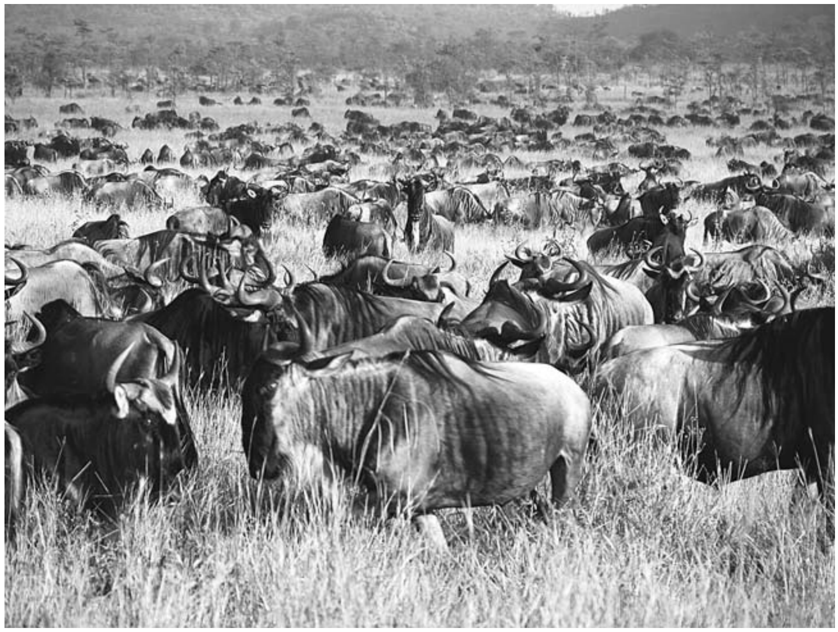

Plate 1. Serengeti National Park, Tanzania, was designed to include most of the migratory range of the Serengeti wildebeest herd. Many other protected areas include only a portion of area required by migratory species. Wildlife in such protected areas is especially vulnerable to land use intensification on the surrounding lands. Photo credit: A. Hansen.

Plate 1). Although Serengeti National Park is insufficient to maintain the wildebeest and other migratory mammals within it, the network of wild and semi-wild public and private lands across the Greater Serengeti Ecosystem may be nearly large enough to maintain these populations (Packer et al. 2005; but see Serneels and Lambin 2001). The Greater Everglades Ecosystem has been defined to encompass the massive contiguous area of freshwater slowly flowing seaward in southern Florida. Everglades National Park includes only a portion of this large watershed and ecological processes within it are strongly influenced by unprotected lands higher in the watershed (NAS 2003). The Greater Yellowstone Ecosystem, including Yellowstone National Park, was defined largely by gradients in topography, climate, and soils, and the resulting movement of wildfire and organisms (Keiter and Boyce 1991, Hansen et al. 2002, Noss et al. 2002). Centered on the Yellowstone Plateau and surrounding mountains, natural disturbance regimes and organisms move across the elevational gradient from valley bottoms to high mountains in response to climate and vegetation productivity (Fig. 2). In these cases, knowledge of the spatial domain of strong ecological interactions between protected areas and the surrounding areas has allowed for specification of the larger effective ecosystem. The term "greater ecosystem" is often used to describe these protected-area-centered ecosystems (Keiter and Boyce 1991).

Recognizing that protected areas are often parts of larger ecosystems helps to clarify the effects of land use. Agriculture, settlement, and other human land uses in the unprotected part of the ecosystem may alter the flows of energy, materials, and organisms across the ecosystem in ways that change ecological functioning within the reserve (Fig. 1b–e). If, for example, the portion of the ecosystem where wildfire tends to ignite is converted agriculture, fire may less frequently spread into the protected area and alter vegetation succession. Similarly, if land use decreases the area of suitable habitats for a wildlife population below some threshold, the population size may fall to the point where extinction is likely. Moreover, land use near a protected area may introduce novel disturbances to which the ecosystem is not adequately adapted. Human hunting and intense outdoor recreation are examples. Given that human land use is rapidly expanding and intensifying in the unprotected parts of many protected area ecosystems, it is critical that we better understand its effects. Knowledge of the mechanisms connecting land use to protected areas can provide an objective basis for defining the spatial domain of the effective ecosystem encompassing protected areas and for managing the unprotected lands to maintain ecological function and biodiversity within protected areas.

Mechanisms Linking Land Use to Protected Areas

Advances in ecological theory have allowed increased understanding of how the spatial patterning across landscapes and regions influences local ecosystems (Turner et al. 2001). Island biogeography, species–area relationships, metapopulation dynamics, disturbance ecology, and landscape ecology have increasingly been applied to questions of conservation biology, including

TABLE 1. General mechanisms by which land use surrounding protected areas alters ecological processes within reserves.

General mechanism and type	Description	Examples
Change in effective size of reserve		
Minimum dynamic area	Temporal stability of seral stages is a function of the area of the reserve relative to the size of natural disturbance.	Hurricanes in Puerto Rico (Shugart 1984).
Species–area effect	As wild habitats in surrounding lands are destroyed, the functional size of the reserve is decreased and risk of extinction in the reserve is increased.	Fragmented forests in Kenya (Brooks et al. 1999); harvest of primary forest outside Calakmul Biosphere Reserve, Mexico (Vester et al. 2007).
Trophic structure	Characteristic spatial scales of organisms differ with trophic level such that organisms in higher levels are lost as ecosystems shrink.	Loss of predators on Barro Colorado Island (Terborgh et al. 2001).
Change in ecological flows into and out of reserve		
Initiation and run-out zones	Key ecological processes move across landscapes. Initiation and run-out zones for disturbance may lie outside reserves.	Fire in Yellowstone National Park (Hansen and Rotella 2001).
Location in watershed or airshed	Land use in upper watersheds or airsheds may alter flows into reserves lower in the watershed or airshed.	Rainfall in Monte Verde cloud forest (Lawton et al. 2001).
Loss of crucial habitat outside of reserve		
Seasonal and migration habitats	Lands outside of reserves may contain unique habitats that are required by organisms within reserves. Organisms require corridors to disperse among reserves or to migrate from reserves to ephemeral habitats.	Large mammals in the Greater Serengeti (Serneels and Lambin 2001); antelope in Greater Yellowstone (Berger 2004).
Population source–sink habitats		
Increased exposure to humans at park edge	Unique habitats outside of reserves are population source areas required to maintain sink populations in reserves.	Birds around Yellowstone National Park (Hansen and Rotella 2002).
Hunting/poaching; exotics/disease	Negative human influences from the reserve periphery extend some distance into protected areas.	Eurasian badgers in Donana Park (Revilla et al. 2001); spread of disease from pets to lions in Serengeti National Park (Packer et al. 1999).

the design of nature reserves (Pressey et al. 1993, Noss and Cooperrider 1994, Prendergast et al. 1999). These bodies of theory can also be applied to understanding how changes in the unprotected parts of greater ecosystems may influence protected areas. Here we synthesize across these bodies of theory to develop a simple conceptual framework for understanding how changes surrounding protected areas alter the ecological processes within them. According to our framework, four general mechanisms link human land uses with ecological function within protected areas. These mechanisms involve effective size of the ecosystem, flows of ecological process zones, crucial habitats, and exposure to humans at reserve edges (Table 1). We will describe, for each of mechanisms, the various forms in which they may be expressed, the conceptual basis, and illustrative examples.

Effective size of ecosystem

We refer to "effective size" of the ecosystem as the area that includes ecological processes and organisms integral to the protected area. This often is correlated with the area of wild and semi-wild habitats within and surrounding the protected area. By reducing this effective size, land use can negatively influence both ecological processes and community diversity and structure (Fig. 1b).

Minimum dynamic area.—Island biogeography theory suggests that the number of species in a nature reserve results from the balance between colonization and extinction. If protected areas are increasingly isolated from external colonization sources, "extinction will then become the dominant population process affecting equilibrium in reserves and species numbers will decline to a new level," according to Pickett and Thompson (1978:28). Hence it is critical to maintain recolonization sources within protected areas. Natural disturbance is a key force in driving patch dynamics within and among protected areas and resources available to organisms. Landslides, floods, wildfires, and hurricanes initiate succession and maintain resources for species associated with each seral stage. Bormann and Likens (1979) used the term "shifting steady-state equilibrium" to define landscapes where disturbance was adequate to maintain each seral stage in relatively constant proportion over time. The location of disturbance shifts across the landscape over time, but the representation of early- and late-seral patches across the landscape remains within a steady state. Such landscapes can support relatively high numbers of organisms because recolonization sources are continuously maintained for species requiring either early- or late-seral conditions.

Pickett and Thompson (1978:27) defined "minimum dynamic area" as "the smallest area with a natural disturbance regime, which maintains internal recolonization sources, and hence minimizes extinction." In other words, minimum dynamic area is the smallest area within which the natural disturbance regime maintains a shifting steady-state equilibrium.

As land use change reduces the effective size of the ecosystem containing a protected area, the ecosystem is increasingly likely to fall below the minimum dynamic area (Baker 1989). In this case, the protected area itself will be too small to maintain a dynamic steady-state equilibrium under the influence of natural disturbance. At this point, recolonization sources for species are lost and extinction rates will rise. How big does an ecosystem need be to maintain a dynamic steady-state equilibrium? Shugart (1984) and Baker (1992) suggested that a landscape needs to be at least 50 times larger than the area of the largest disturbance to maintain this equilibrium.

We are not aware of any studies that have documented a change in effective ecosystem size resulting in loss of minimum dynamic area and loss of species within a protected area. Baker (1989) found that the Boundary Waters Canoe Area in northern Minnesota was not large enough to maintain a fire-induced steady-state equilibrium. Wimberly et al. (2000) found that the minimum dynamic area induced by fire in the Oregon Coast Range in pre-European settlement times was larger than the old-growth forest reserves maintained today. McCarthy and Lindenmayer (1999, 2000) used spatially explicit population viability models to estimate the minimum size of protected areas needed to maintain viable populations of forest marsupials in Australia under various disturbance regimes.

Species–area effects.—A well-known tenet of island biogeography theory is that the number of species that are found on an oceanic island or in a habitat fragment is a function of its area. A large body of empirical evidence indicates that the number of species (termed species richness), S, increases with area A, according to the equation $S = cA^z$, where c and z are constants (e.g., Rosenzweig 1995). Hence, species richness increases with island or habitat area, at a decelerating rate for larger areas. The primary explanation is that a given species is less likely to go extinct if the area of suitable habitat is large enough to provide the resources to allow for a population size larger than a minimum viable population below which risk of extinction is elevated (Pimm et al. 1988).

The species–area relationship has been used to predict the consequences of reducing the size of a habitat through conversion to intensive land uses (for a review, see Cowlishaw 1999). A contraction in habitat from its original area to its new area is predicted to lead to a decline from the original number of species to a new total based on the size of the fragment. This number is expected to be further reduced through time as the effects of isolation lead to local extinctions within the fragment, due to small population sizes. In a test of this approach, Brooks et al. (1999) surveyed birds in upland forest fragments in Kenya. They compared current species richness for forest birds with that from the time prior to habitat fragmentation, using museum records. They found that each of the five habitat fragments had undergone extinctions of forest birds and that the number of extinctions was close to that predicted, based on the change in area.

Following habitat fragmentation, the relaxation to the new reduced species richness may take decades to centuries or more (Burkey 1995, Brooks et al. 1999). The term "extinction debt" is used to denote the number of species that are expected to become extinct as the community adjusts to a new, smaller, area of habitat. In the New World tropics, deforestation is sufficiently recent that few extinctions have yet occurred. In confirmation of the species–area approach, however, Brooks and Balmford (1996) and Brooks et al. (1997) found that the predicted number of extinctions for Atlantic forests of South America and insular Southeast Asia closely matched the numbers of species currently listed as threatened with extinction. In tropical forests of Africa, Cowlishaw (1999) predicted that current deforestation will eventually result in the extinction of >30% of the forest primate fauna in each of several countries.

The implication of the species–area relationship for protected areas is that the number of species in a protected area will decline as the effective size of the reserve is reduced through destruction of the unprotected habitats surrounding the reserve. This point was illustrated by Pimm and Raven (2000). They focused on biodiversity hotspots around the world identified by Myers et al. (2000). These hotspots have already suffered disproportionate loss of primary vegetation, meaning that the many species they contain are under particular threat of extinction. Using the species–area relationship, Pimm and Raven (2000) predicted that more species would be lost if only hotspots now in a protected status were saved than if all hotspot habitats (both inside and outside protected areas) were saved.

The species–area approach was applied to three of the case study locations reviewed in this Invited Feature: Maasai East Africa, Southern Yucatán, and Greater Yellowstone (H. L. Rustigian et al., *unpublished manuscript*). Habitats that had been deforested and converted to agriculture, settlements, or rural dispersed homes

TABLE 2. Loss of habitat since pre-European settlement times and predicted extinctions of birds and mammals under current remaining habitat and habitat remaining if all unprotected lands are converted to human land uses.

				No. (and %) species predicted extinct	
Location	Total area (km^2)	Original habitat intact	Original richness	Current	Under full conversion
Maasailand, East Africa	193 405	55%	756	107 (14.2%)	262 (34.7%)
Greater Yellowstone, USA	95 363	89%	284	14 (4.9%)	26 (9.2%)
Mayan Forest, southern Yucatán Peninsula	120 109	70%	315	26 (8.3%)	75 (23.8%)

Notes: Data are from H. L. Rustigian et al. (*unpublished manuscript*). Richness is the number of species.

since pre-European settlement times were considered not suitable for native bird and mammal species. Based on loss of habitats from pre-European settlement times, the ecosystem around each park, they predicted a loss of 5–14% of species among the sites (Table 2). If all unprotected habitats were converted to human land uses, 9–35% of species were predicted to be lost.

A limitation of the species–area approach to estimating fragmentation effects is that species differ in their tolerance to the type and intensity of human land use. Many native species find suitable habitat in human-altered landscapes and some of these species become more abundant under certain land uses (McKinney 2002). The approach will be most effective if it is applied to species that are unable to tolerate the human-induced changes to the unprotected portion of the ecosystem. The approach will also be more accurate if the quality of lost habitats is considered. Vester et al. (2007) found that tall primary forest has been disproportionately destroyed in the southern Yucatán region. Several species of trees and butterflies are uniquely associated with this forest type and may have been disproportionately affected by its loss in area.

Trophic structure.—A third consequence of reducing the effective size of nature reserves is an altered representation of organisms at various levels of the food chain. Perhaps the most typical case is the loss of high-level predators and the release of meso-level predators or herbivores. Home range size and density are associated with level in the food chain. Top predators tend to have relatively large home range requirements and low densities. Consequently, they are particularly sensitive to extinction as effective reserve size decreases (Schonewald-Cox 1988, Woodroffe and Ginsberg 1998).

Perhaps the most direct evidence that trophic structure in protected areas varies with effective size of ecosystem comes from correlational studies of species extinction in protected areas of differing size. Rivard et al. (2000) found that extinction rates of mammals in Canadian national parks were associated both with park area and with the extent of intense land use outside of parks. Moreover, they found that species with large home ranges, typical of species at higher trophic levels, were more likely to suffer extinction. Evidence for similar patterns in aquatic systems comes from Post et al. (2000), who studied trophic structure in 25 north-temperate lakes. They found that the length of food chains was positively related to ecosystem size (size of the lake). Specifically, higher trophic levels were more commonly found in larger lakes.

In some systems, these top predators influence the abundance of organisms lower in the food chain with cascading effects throughout the ecosystem. Hence, loss of the top predators may allow meso predators or herbivores to become increasingly abundant. This effect on trophic structure was documented in a study of island habitat fragments created by a water impoundment project in Venezuela (Terborgh et al. 2001). Vertebrate predators went extinct on small- and medium-sized islands but remained on larger islands. Densities of seed predators and herbivores were 10–100 times higher than those on the mainland, probably due to the release from predation. These changes cascaded through the food chain, resulting in severe reductions in densities of canopy tree seedlings and saplings.

Trophic cascades associated with top predators are also suggested in the Greater Yellowstone Ecosystem. The recent reintroduction of the wolf (*Canus lupis*), a top predator that had been extinct for 60 years, appears to be expanding the scavenger community, reducing mesocarnivores and ungulate population sizes, releasing the riparian plant community that was overbrowsed by ungulates, and allowing for expansion of riparian-dependent bird communities (Ripple and Beschta 2004).

Thus, reduction in the effective size of a protected area is predicted to result in losses in species due to change in landscape dynamics, species–area effects, and loss of top carnivores. As the unprotected lands around nature reserves are increasingly converted to intense human land uses, effective ecosystem size is reduced. For relatively few protected areas do we know the effective size of the ecosystem and the rate of loss to human land use. Rustigan et al. (*unpublished data*) found that, for three case study landscapes, the loss rate since presettlement times was substantial: 11%, 30%, and 45% for Greater Yellowstone, Mayan Forest, and Greater Serengeti ecosystems have been converted to intense human uses.

Ecological process zones

Just as organisms move across landscapes at characteristic scales, ecological processes result in flows of energy and materials along predictable pathways. These flows may be important to ecological function in influencing local ecological processes such as primary productivity or habitat suitability. To the extent that land use conversion and intensification alters ecological flows across the landscape, it may impact the ecological functioning and biodiversity within protected areas (Fig. 1c).

Disturbance initiation and run-out zones.—Disturbances tend to be initiated in particular landscape settings and move to other locations in the landscape. Interactions between the location where disturbance gets started (initiation zones) and locations where disturbances move to (run-out zones) influence the nature of the disturbance regime in an area (Baker 1992). In southwestern Montana, for example, lightning strikes occur across the landscape, but more frequently ignite fires in dry valley-bottom grasslands than in moist conifer forests in the uplands (Arno and Gruell 1983). These fires then spread upslope to the conifer forests. Thus, the juxtaposing of grasslands and conifer forests strongly influences the regional fire regime. Local disturbance regimes can best be maintained in protected areas that include the disturbance initiation zones within their boundaries (Baker 1992). In the case of the Montana example, a protected area placed only in the upland conifers may suffer more or less frequent fire, depending on the management of the valley-bottom grasslands outside of the protected area.

It is also important to include disturbance run-out zones within the boundaries of protected areas. Run-out zones may contain unique abiotic conditions and habitat patterns important to ecological processes and organisms. For example, flood severity often increases from headwaters to large floodplains. The large scours and bare gravel bars and the mosaic of seral stages that form on floodplains support high levels of biodiversity (Saab 1999). A protected area that does not contain this disturbance run-out zone will not include these unique riparian vegetation communities. In protected areas that omit either the initiation or run-out zones, human manipulation of disturbance may be required to maintain landscape patterns and organisms (Baker 1992, Arcese and Sinclair 1997).

Location in watershed or airshed.—Protected areas may be heavily influenced by hydrologic flows and weather systems. For example, protected areas throughout the world are threatened by cumulative alterations in hydrologic connectivity within the larger landscape (Pringle 2001). Humans are altering hydrologic flows directly by dams, water diversions, groundwater extraction, and irrigation, and indirectly by altering land cover, which may change rates of transpiration, runoff, and soil storage. These flows of water transport energy, nutrients, sediments, and organisms.

The location of a given protected area within a watershed, relative to regional aquifers and wind and precipitation patterns, can play a key role in its response to human disturbance transmitted through the hydrologic cycle. Protected areas located in middle and lower watersheds often experience altered flow regimes and inputs of exotic organisms and pollution from upstream. The Colorado River within Grand Canyon National Park, for example, has undergone a dramatic transformation due to dams and intense land use in the headwaters of the watershed (Cohn 2001). Altered water temperatures and loss of flood deposition of sediments have changed habitats, leading to a substantial reduction of native fishes. Waterborne seeds of exotic plants such as saltcedar (*Tamarix* spp.) have led to entirely new riparian communities and loss of native riparian species such as the Willow Flycatcher (*Empidonax traillii*).

Protected areas in upper watersheds, in contrast, are vulnerable to land use lower in the watershed. These human activities may provide vectors for exotic species and disease to penetrate the upper watershed. They may also result in genetic isolation of populations in headwaters. In the northern Rocky Mountains, USA, native west-slope cutthroat trout (*Oncorhynchus clarki lewisi*) historically occupied entire watersheds. Subpopulations in headwaters may have been dependent on source populations in lowlands. Mainstream populations were forced to extinction by the introduction of exotic trout species and possibly by habitat changes associated with irrigation and other intense land uses. Consequently, populations surviving in headwater streams in national parks are subject to a high probability of extinction, probably because they no longer receive immigrants from source populations in lowland streams (Shepard et al. 1997).

This discussion of watershed effects also applies to airsheds. Change in regional land use may alter climate and nutrient deposition within downwind protected areas considerable distances away (Lawton et al. 2001). Tropical montane cloud forests in Central America depend upon prolonged immersion in clouds. Clearing of forests in Costa Rica's Caribbean lowlands appears to have reduced cloud cover and increased cloud height in cloud forests, such as in Monte Verde National Park, altering ecosystem function and possibly contributing to the decline of 20–50 species of frogs and toads in Monte Verde National Park (Nair et al. 2003).

Such changes in ecosystem processes are especially difficult for managers of protected areas to perceive because they may result from changes in the air or watershed at long distances from the protected area.

Crucial habitats

Protected areas may not contain the full suite of habitats required by organisms to meet their annual life history requirements. Seasonally important habitats may lie outside the boundaries of protected areas. Land use in the unprotected portion of ecosystems may alter or destroy these seasonal habitats, as well as movement corridors connecting these habitats to protected areas (Fig. 1d).

This situation is common because of the nonrandom location of protected areas relative to biophysical conditions and habitats. Protected areas are often located in relatively harsh biophysical settings and represent the colder or hotter, drier, more topographically complex, and/or less productive portions of the broader ecosystems in which they lie (Scott et al. 2001). Intense human land use, in contrast, is often centered on more equitable and productive landscape settings (Seabloom et al. 2002, Huston 2005). Consequently, the unprotected portions of ecosystems often contain habitats crucial for organisms that reside within the protected areas for portions of the year. Intense land use may be disproportionately centered on these unprotected crucial habitats (Hansen and Rotella 2002).

Seasonal and migration habitats.—Animals often move across the landscape seasonally to obtain required resources. For protected areas at higher elevations, key winter ranges are often outside the boundaries of protected areas. Similarly, protected areas in more arid regions often do not contain wet-season habitats. Land use may alter these unprotected seasonal habitats or the movement pathways between seasonal habitats.

Populations of several large-mammal species within the Maasai Mara Reserve and Amboseli National Park in Kenya have declined in abundance during the past 30 years in the face of rapid intensification of land use in the surrounding regions (A. J. Hansen et al., *unpublished report*). Of the 15 species analyzed, eight species in the Massai Mara Reserve and one species in Amboseli declined significantly during this time. The declines were severe for several species and ranged from 0.7% to 2.5% of the population size per annum. These population changes were statistically associated with human use factors in the wet-season habitats outside of the protected area boundaries. In tropical forests of Borneo, Indonesia, long-distance migrations of bearded pigs have been disrupted by the logging of the dipterocarp trees whose fruits are prime food sources for the pigs (Curran et al. 1999). Berger (2004) documented that the 225-km movement corridor for pronghorn antelope (*Antilocapra americana*) between summer and winter range in Greater Yellowstone passes through a 1 km wide bottleneck that is now threatened with natural gas development.

Population source–sink habitats.—The crucial habitats outside of protected areas may be especially rich in resources and may act as population "source" areas. These habitats may allow subpopulations to produce surplus offspring that disperse to less productive habitats in protected areas and allow persistence of the subpopulations in the reserves. For example, Hansen and Rotella (2002) found that bird populations in the Greater Yellowstone Ecosystem were concentrated in small hotspots in productive, lowland settings outside protected areas. These source habitats have been disproportionately used for agriculture and rural home sites (Gude et al. 2007). This intense land use has converted these low-elevation source areas for the populations to sink areas and reduced the viability of subpopulations in the more marginal habitats in protected areas. Similarly, Arcese and Sinclair (1997) suggested that most of Serengeti National Park is a sink for the lion population and that the species is maintained there because of connectivity with the Ngorongoro Conservation Area, which is a population source area for lion.

The migratory movements of many organisms across greater ecosystems are often quite obvious to park managers and local people. Hence, the problem of unprotected seasonal habitats has received considerable attention in many regions. Designation and protection of migration corridors is increasingly widely used to minimize or mitigate conflicts between human land use and migrating wildlife (e.g., Miller et al. 2001).

Proximity to humans

Human presence on the periphery of protected areas may cause changes in ecosystem processes and biodiversity that extend varying distances into the protected area (Fig. 1e). Some of these edge effects result in habitat change. For example, clearing of forests to the edge of the protected area boundary may lead to elevated disturbance rates and high levels of forest mortality within the forest reserve (Laurance et al. 2000).

Other types of edge effects do not cause visible changes in habitat, but have strong influences on organisms in protected areas nonetheless. Hunting and poaching often extend the footprint of human settlements into adjacent protected areas (Escamilla et al. 2000, Revilla et al. 2001). For example, on the western border of Serengeti National Park, poaching was estimated to extend up to 25 km into the park (Campbell and Hofer 1995). Exotic organisms and disease also may spread from border communities into protected areas. Bison (*Bison bison*) in Yellowstone National Park contracted brucellosis while commingling with livestock in winter range outside of the park (Yellowstone National Park 1997). This has led to a substantial management challenge now that the disease has been largely eradicated from livestock herds in the United States. Similarly, lions in Serengeti National Park underwent dramatic population declines from the canine distemper that they contracted from domestic dogs living outside the park (Packer et al. 1999). Human recreation is sometimes elevated near borders of protected areas and may displace wildlife (Hansen et al. 2005).

Many of these edge effects are proportional to the density of the adjacent human population (Woodroffe and Ginsberg 1998, Brashares et al. 2001). Hence, these effects may be increased under human population growth around protected areas.

Implications for Conservation and Management

This framework of mechanisms linking land use with protected areas can enhance the various ongoing conservation and management approaches. The frame-

TABLE 3. Criteria for managing regional landscapes to reduce the impacts of land use change outside of protected areas on ecological processes and biodiversity within reserves.

Mechanism	Type	Design criteria
Change in effective size of reserve	species–area effect; minimum dynamic area; trophic structure	maximize area of functional habitats
Changes in ecological flows into and out of reserve	disturbance initiation and run-out zones; placement in watershed or airshed	identify and maintain ecological process zones
Loss of crucial habitat outside of reserve	ephemeral habitats; dispersal or migration habitats; population source sink habitats	maintain key migration and source habitats
Increased exposure to human activity at reserve edge	poaching; displacement; exotics/disease	manage human proximity and edge effects

work provides a conceptual basis for: (1) mapping the boundaries of the effective ecosystem encompassing a protected area; (2) monitoring and assessing management effectiveness; (3) systematic conservation planning and management of the effective ecosystem; and (4) assessing vulnerability of protected areas to land use change. We will discuss each of these applications.

Ecosystem boundaries

Managers need to be able to quantify the boundaries of the effective ecosystem encompassing a protected area in order to know where to monitor land use change, assess management effectiveness, and implement regional conservation strategies to maintain the protected area. The ecosystem boundaries should include the areas that are strongly connected to the protected area in ecological processes or organism movements and population processes. The mechanisms framework provides a conceptual basis for mapping these connections and identifying the boundaries of the effective ecosystem. The area of seminatural habitats contributing to effective ecosystem size can be mapped using remote-sensing techniques (Rogan and Chen 2004). The spatial and temporal dynamics of natural disturbance regimes can be mapped from historic records or projected with computer simulation models (e.g., Baker 1989). Movements of organisms can be quantified through use of telemetry and other methods (e.g., Berger 2004). Mapping of population processes and source–sink dynamics requires both field studies and simulation modeling (e.g., Hansen and Rotella 2002). Quantification of human edge effects can be done with human surveys and other assessment methods (Campbell and Hoffer 1995). In addition to these quantitative methods, expert opinion often will be needed to delineate ecologically meaningful boundaries.

Management effectiveness and monitoring

After a period of focus on the creation of new protected areas, many managers and conservationists are attending to the assessment of how well existing protected areas are working. For example, the World Commission on Protected Areas (WCPA) has developed a six-step process for assessing management effectiveness. "The process begins with establishing the *context* of existing values and threats, progresses through *planning* and allocation of resources (*inputs*), and, as a result of management actions (*process*), eventually produces goods and services (*outputs*) that result in impacts or *outcomes*" (Hockings 2003:826). This approach may be based on results of questionnaires of managers and other stakeholders or on quantitative data from ecological measurement. Our framework of mechanisms provides a conceptual basis for portions of the process. "Context" can be evaluated by assessing threats from land use relative to the places and processes identified in our ecological mechanisms. "Planning" and management "process" can be aimed at maintaining the connections and functions identified by our mechanisms.

The U.S. National Park Service and the Canadian Park Service (Parks Canada Agency 2005) have each established inventory and monitoring (I&M) programs aimed at assessing the condition of parks and determining management effectiveness. Within the U.S. National Park Service I&M Program, our mechanisms framework has been used to guide selection of monitoring indicators, delimitate the effective ecosystem, and guide analysis of trends in threats and ecological response (D. A. Jones et al., *unpublished manuscript*).

Regional management

It is apparent that many protected areas may become degraded by land use and other factors occurring in the unprotected parts of the surrounding ecosystem. Thus, maintaining protected areas often will require some level of conservation-oriented management in the unprotected portion of the ecosystem. "Systematic conservation planning" (Margules and Pressey 2000) provides a coordinated approach for assessment and management across regional landscapes. Our mechanisms framework provides design criteria for regional management (Table 3). Knowledge of land use patterns, the spatial dynamics of these ecological mechanisms, and the responses of ecological processes provide a context to identify places in the unprotected parts of the ecosystem that are most critical for maintaining ecological function within protected areas. Management should focus on maintaining effective ecosystem size, ecological process zones, crucial habitats for organisms, and on minimizing negative human edge effects. Coupled with understand-

TABLE 4. Varying effects of different land use types on ecological mechanisms altering reserves.

Type of land use change	Effective reserve size	Ecological process zones/flows	Crucial habitats	Edge effects
Resource extraction				
Logging	x	x	x	
Mining		x	x	
Poaching				x
Food production				
Subsistence farming				x
Small-scale farming	x	x	x	x
Large-scale commercial farming	x	x	x	x
Recreation				
Tourism				x
Infrastructure				
Roads/other transport			x	x
Dams		x	x	
Residential/commercial				
Settlements				x
Urban/suburban	x	x	x	x

Note: An "x" indicates that a land use type is likely to invoke the specified ecological mechanism and to influence ecosystem function and biodiversity within protected areas.

ing of the socioeconomic dynamics in the region (DeFries et al. 2007), the mechanisms offer a comprehensive approach for understanding and managing these vitally important regions to maintain ecological function while minimizing negative impacts on surrounding human communities.

Vulnerability of protected areas to surrounding land use

With limited resources for conservation, it is necessary to identify which protected areas are most vulnerable to land use change so that mitigation strategies can be focused on these areas (Wilson et al. 2005). Three classes of factors that may influence the vulnerability of a protected area to land use intensification are: the ecological properties of the protected area and surrounding ecosystem; the type and rates of land use conversion and intensification; and the properties of the surrounding human communities. We suggest that the most vulnerable protected areas will be those with the following characteristics.

1) The protected area is small or poorly placed relative to minimum dynamic area of disturbance; shape of species–area curves; biophysical gradients and the resulting areas of organism movements; and watershed size.

2) The protected area is in close proximity to dense human populations, intense land use in critical portions of the ecosystem, or is likely to come in close proximity under future land use change.

3) The surrounding human community lacks incentives or resources for forwarding ecological goals of protected areas.

The first point follows from the fact that the spatial extent of ecosystem processes may differ from place to place. For example, spatial patterns of precipitation may determine whether organisms migrate over small or large areas. Thus, the key to assessing vulnerability of protected areas is to evaluate not the absolute size of the area, but its size relative to the effective ecosystem it exists within. Quantitative assessment of the spatial extent of biophysical factors, hydrologic flows, disturbance, and organism movements relative to size and location of the protected area provides a context for assessing the vulnerability of the protected area to land use change in the unprotected portion of the ecosystem.

The intensity and type of land use in surrounding lands also differs among protected areas. Parks surrounded by intense land uses, such as urban and suburban, are more vulnerable than those set in a wilderness context. Also, land use types differ in their likely influence on protected areas. Land uses such as commercial farming may elicit all four of the mechanisms previously described, whereas others such as tourism or poaching may involve a single mechanism (Table 4).

The socioeconomic fabric of surrounding human communities probably also influences the vulnerability of protected areas. Protected areas located in areas where surrounding communities rely on bushmeat or forest products are likely to be more vulnerable. Protected areas also vary in the enforcement of policies to protect reserves (Bruner et al. 2001). For example, elephant populations fared better in African countries that were able to control poaching prior to the ivory ban in the 1980s (Leakey and Morell 2001). Protected areas surrounded by human communities that benefit from them may be less vulnerable due to a higher likelihood of regional-scale management to forward the goals of the protected area (Rasker and Hansen 2000).

Finally, we suggest that the confluence of these factors has a larger effect on the protected area than the additive effect of the individual factors. With further refinement and testing, such criteria could provide a basis for evaluating the global network of protected areas and for identifying those that are the highest priority of conservation attention, based on vulnerability to land use change. Within a regional context, the principles also can be applied to strategic land use management to conserve elements of the landscape most crucial to reserve function, while allowing land use to fulfill human needs on those portions of the landscape less crucial to the functioning of reserves.

The case studies in this Invited Feature provide examples of regional assessments and management implications around several protected areas in varying ecological and socioeconomic settings. The concluding paper by DeFries et al. (2007) explores in detail the interactions between protected areas and local people and opportunities for achieving regional-scale management.

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Literature Cited

Agee, J. K., and O. R. Johnson. 1988. Ecosystem management for parks and wilderness. University of Washington Press, Seattle, Washington, USA.

Arcese, P., and A. R. E. Sinclair. 1997. The role of protected areas as ecological baselines. Journal of Wildlife Management 61:587–602.

Arno, S. F., and G. E. Gruell. 1983. Fire history at the forest–grassland ecotone in southwestern Montana. Journal of Range Management 36:332–336.

Baker, W. L. 1989. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. Ecology 70:23–35.

Baker, W. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecology 7:181–194.

Berger, J. 2004. The last mile: How to sustain long-distance migrations in mammals. Conservation Biology 18:320–331.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.

Brashares, J. S., P. Arcese, and M. K. Sam. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society of London B 268:2473–2478.

Brooks, T. M., and A. Balmford. 1996. Atlantic forest extinctions. Nature 380:115.

Brooks, T. M., S. L. Pimm, and N. J. Collar. 1997. Deforestation predicts the number of threatened birds in insular Southeast Asia. Conservation Biology 11:382–394.

Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conservation Biology 5:1140–1150.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land use trends in the conterminous U.S., 1950–2000. Ecological Applications 15:1851–1863.

Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. Science 291:125–128.

Buechner, M. 1987. Conservation in insular parks: Simulation models of factors affecting the movement of animals across park boundaries. Biological Conservation 41:57–76.

Burkey, T. V. 1995. Extinction rates in archipelagoes: implications for populations in fragmented habitats. Conservation Biology 9:527–541.

Campbell, K., and H. Hofer. 1995. People and wildlife: spatial dynamics and zones of interactions. Pages 534–570 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: Dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Chandrashekara, U. M., and S. Sankar. 1998. Ecology and management of sacred groves in Kerala, India. Forest Ecology and Management 112:165–177.

Chown, S. L., B. J. van Rensburg, K. J. Gaston, A. S. L. Rodrigues, and A. S. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. Ecological Applications 13: 1233–1241.

Cohn, J. P. 2001. Resurrecting the dammed: a look at Colorado River restoration. BioScience 51:998–1004.

Cowlishaw, G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conservation Biology 13:1183–1193.

Craighead, F. 1979. Track of the grizzly. Sierra Club Books, San Francisco, California, USA.

Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita, and H. Haeruman. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. Science 286:2184–2188.

Dasmann, R. F. 1988. Biosphere reserves, buffers, and boundaries. BioScience 38:487–489.

DeFries, R., A. J. Hansen, A. C. Newton, M. Hansen, and J. Townshend. 2005. Isolation of protected areas in tropical forests over the last twenty years. Ecological Applications 15: 19–26.

DeFries, R., A. Hansen, B. L. Turner, R. Reid, and J. Liu. 2007. Land use change around protected areas: management to balance human needs and ecological function. Ecological Applications 17:1031–1038.

Ervin, J. 2003*a*. Protected area assessments in perspective. BioScience 53:819–822.

Ervin, J. 2003*b*. Rapid assessment of protected area management effectiveness in four countries. BioScience 53:833–841.

Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability and hunting in the tropical forest of Calakmul, Mexico. Conservation Biology 14:1592–1601.

Grumbine, E. 1990. Protecting biological diversity through the greater ecosystem concept. Natural Areas Journal 10: 114–120.

Grumbine, E. 1994. What is ecosystem management? Conservation Biology 54:28–38.

Gude, P. H., A. J. Hansen, and D. A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. Ecological Applications 17:1004–1018.

Gude, P. H., A. J. Hansen, R. Rasker, and B. Maxwell. 2006. Rate and drivers of rural residential development in the Greater Yellowstone. Landscape and Urban Planning 77: 131–151.

Hansen, A. J., R. DeFries, and W. Turner. 2004. Land use change and biodiversity: a synthesis of rates and consequences during the period of satellite imagery. Pages 277–299 *in* G. Gutman and C. Justice, editors. Land change science: observing, monitoring, and understanding trajectories of change on the earth's surface. Springer-Verlag, New York, New York, USA.

Hansen, A. J., R. Knight, J. Marzluff, S. Powell, K. Brown, P. Hernandez, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, research needs. Ecological Applications 15:1893–1905.

Hansen, A. J., R. Rasker, B. Maxwell, J. J. Rotella, A. Wright, U. Langner, W. Cohen, R. Lawrence, and J. Johnson. 2002. Ecology and socioeconomics in the New West: a case study from Greater Yellowstone. BioScience 52:151–168.

Hansen, A. J., and J. J. Rotella. 2001. Nature reserves and land use: implications of the "place" principle. Pages 57–75 *in* V. Dale and R. Haeuber, editors. Applying ecological principles to land management. Springer-Verlag, New York, New York, USA.

Hansen, A. J., and J. J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology 16:1–12.

Hockings, M. 2000. Evaluating protected area management: a review of systems for assessing management effectiveness of protected areas. University of Queensland School of Natural and Rural Systems Management, Occasional Paper 7(3).

Hockings, M. 2003. Systems for assessing the effectiveness of management in protected areas. BioScience 53:832–832.

Huston, M. A. 2005. Environmental drivers of land use change: implications for biodiversity. Ecological Applications 15: 1864–1878.

Keiter, R., and M. Boyce. 1991. The Greater Yellowstone Ecosystem. Yale University Press, New Haven, Connecticut, USA.

Laurance, W. F., P. Delamonica, S. G. Laurance, H. L. Vasconcelos, and T. E. Lovejoy. 2000. Rainforest fragmentation kills big trees. Nature 404:836.

Lawton, R. O., R. S. Nair, R. A. Pielke, Sr., and R. M. Welch. 2001. Climatic impacts of tropical lowland deforestation on nearby montane cloud forests. Science 294:584–587.

Leakey, R., and V. Morell. 2001. Wildlife wars: My fight to save Africa's national treasures. St. Martin's Press, New York, New York, USA.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

McCarthy, M. A., and D. B. Lindenmayer. 1999. Incorporating metapopulation dynamics of greater gliders into reserve design in disturbed landscapes. Ecology 80:651–667.

McCarthy, M. A., and D. B. Lindenmayer. 2000. Spatially-correlated extinction in a metapopulation model of Leadbeater's Possum. Biodiversity and Conservation 9:47–63.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

Meffe, G. K., M. J. Groom, and C. R. Carroll. 2004. Ecosystem approaches to conservation: responses to a complex world. Pages 467–508 *in* M. J. Groom, G. K. Meffe, and C. R. Carroll, editors. Principles of conservation biology. Third edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Miller, K., E. Chang, and N. Johnson. 2001. Defining common ground for the Mesoamerican Biological Corridor. World Resources Institute, Washington, D.C., USA.

Mustard, J., R. DeFries, T. Fisher, and E. F. Moran. 2004. Land use and land cover change pathways and impacts. Pages 411–430 *in* G. Gutman, J. Janetos, C. O. Justice, E. F. Moran, J. Mustard, R. Rindfuss, D. L. Skole, B. L. Turner, and M. A. Cochrane, editors. Land change science: observing, monitoring, and understanding trajectories of change on the earth's surface. Springer-Verlag, Dordrecht, The Netherlands.

Myers, N., R. A. Mittermeier, G. C. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nair, U. S., R. O. Lawton, R. M. Welch, and R. A. Pielke, Sr. 2003. Impact of land use on Costa Rican tropical montane cloud forests: Sensitivity of cumulus cloud field characteristics to lowland deforestation. Journal of Geophysical Research 108:1–13.

NAS (National Academy of Sciences). 2003. Science and the greater Everglades Ecosystem restoration: an assessment of the critical ecosystem studies initiative. National Academy of Sciences Press, Washington, D.C., USA.

Newmark, W. D. 1985. Legal and biotic boundaries of Western North American national parks: a problem of congruence. Biological Conservation 33:197–208.

Newmark, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North America parks. Nature 325:430–432.

Newmark, W. D. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology 9:512–526.

Newmark, W. D. 1996. Insularization of Tanzanian parks and the local extinction of large mammals. Conservation Biology 10:1549–1556.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience 33:700–706.

Noss, R. F., C. Carrol., K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology 16:895–908.

Noss, R. F., and A.Y. Cooperrider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Washington, D.C., USA.

Packer, C., S. Altizer, M. Appel, E. Brown, J. Martenson, S. J. O'Brien, M. Roelke-Parker, R. Hofmann-Lehmann, and H. Lutz. 1999. Viruses of the Serengeti: patterns of infection and mortality in African lions. Journal of Animal Ecology 68: 1161–1178.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307:390–393.

Parks Canada Agency. 2005. Monitoring and reporting ecological integrity in Canada's national parks. Volume 1: Guiding principles. Parks Canada Agency, Ottawa, Canada.

Parks, S. A., and A. H. Harcourt. 2002. Reserve size, local human density, and mammalian extinctions in the U.S. protected areas. Conservation Biology 16:800–808.

Parrish, J. D., D. P. Braun, and R. S. Unnasch. 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. BioScience 53:851–860.

Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13: 27–37.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757–785.

Pimm, S. L., and P. Raven. 2000. Biodiversity: extinction by numbers. Nature 403:843–845.

Possingham, H. P., K. A. Wilson, S. J. Aldeman, and C. H. Vynne. 2006. Protected areas: goals, limitations, and design. Pages 509–551 *in* M. J. Groom, G. K. Meffe, and C. R. Carroll, editors. Principles of conservation biology. Third edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Post, D. M., M. L. Pace, and N. G. Hairston, Jr. 2000. Ecosystem size determines food-chain length in lakes. Nature 405:147–1049.

Prendergast, J. R., R. M. Quinn, and J. H. Lawton. 1999. The gaps between theory and practice in selecting nature reserves. Conservation Biology 13:484–492.

Pressey, R. L. 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? Conservation Biology 8:662–668.

Pressey, R. L., R. M. Cowling, and M. Rouget. 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. Biological Conservation 112:99–127.

Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. Trends in Ecology and Evolution 8:124–128.

Pringle, C. E. 2001. Hydrologic connectivity and the management of biological reserves: a global perspective. Ecological Applications 11:981–998.

Prospero, J. M., and P. J. Lamb. 2003. . African droughts and dust transport to the Caribbean: climate change implications Science 302:1024–1027.

Rasker, R., and A. J. Hansen. 2000. Natural amenities and population growth in the Greater Yellowstone region. Human Ecology Review 7:30–40.

Revilla, E., F. Palomares, and M. Delibes. 2001. Edge–core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Donana National Park. Conservation Biology 15:148–158.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755–766.

Rivard, D. H., J. Poitevin, D. Plasse, M. Carleton, and D. J. Currie. 2000. Changing species richness and composition in Canadian National Parks. Conservation Biology 14:1099–1109.

Rogan, J., and D. M. Chen. 2004. Remote sensing technology for mapping and monitoring land-cover and land-use change. Progress in Planning 61:301–325.

Rosenzweig, M. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical approach. Ecological Applications 9:135–151.

Schonewald-Cox, C. M. 1988. Boundaries in the protection of nature reserves. BioScience 38:480–486.

Schullery, P. 1997. Searching for Yellowstone: ecology and wonder in the last wilderness. Houghton Mifflin, Boston, Massachusetts, USA.

Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: do they capture the full range of America's biological diversity? Ecological Applications 11:999–1007.

Seabloom, E. W., A. P. Dobson, and D. M. Storms. 2002. Extinction rates under nonrandom patterns of habitat loss. Proceedings of the National Academy of Sciences (USA) 99: 11229–11234.

Serneels, S., and E. Lambin. 2001. Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti-Mara Ecosystem. Journal of Bigeography 28: 391–408.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for west-slope cutthroat trout in the upper Missouri River Basin, Montana. North American Journal of Fisheries Management 17:1158–1172.

Shugart, H. H. 1984. A theory of forest dynamics. Springer-Verlag, New York, New York, USA.

Sinclair, A. R. E. 1995. Serengeti past and present. Pages 3–30 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II. Dynamics, management and conservation of an ecosystem. University of Chicago Press Chicago, Illinois, USA.

Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildlife Society Bulletin 26:399–409.

Stohlgren, T. J. 1998. Rocky Mountains. Pages 473–504 *in* M. J. Mac, P. A. Opler, C. E. Puckett Haecker, and P. D. Doran, Status and trends of the nation's biological resources. U.S. Geological Survey, Washington, D.C., USA.

Terborgh, J., L. Lopez, N. V. Percy, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

TNC (The Nature Conservancy). 2000. The five-S framework for site conservation: A practitioner's handbook for site conservation planning and measuring conservation success. The Nature Conservancy, Arlington, Virginia, USA.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer-Verlag, New York, New York, USA.

UNESCO (United Nations Educational, Scientific, and Cultural Organization). 1974. Task force on criteria and guidelines for the choice and establishment of biosphere reserves. Man and the Biosphere Report Number 22. UNESCO, Paris, France.

Vester, H. F. M., D. Lawrence, J. R. Eastman, B. L. Turner II, S. Calmé, R. Dickson, C. Pozo, and F. Sangermano. 2007. Land change in the southern Yucatán and Calakmul Biosphere Reserve: effects on habitat and biodiversity. Ecological Applications 17:989–1003.

Viña, A., S. Bearer, X. Chen, G. He, M. Linderman, L. An, H. Zhang, Z. Ouyang, and J. Liu. 2007. Temporal changes in giant panda habitat connectivity across boundaries of Wolong Nature Reserve, China. Ecological Applications 17: 1019–1030.

Wilson, K. A., R. L. Pressey, A. N. Newton, M. A. Burgman, H. P. Possingham, and C. J. Weston. 2005. Measuring and incorporating vulnerability into conservation planning. Environmental Management 35:527–543.

Wimberly, M. C., T. A. Spies, C. J. Long, and C. Whitlock. 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. Conservation Biology 14: 167–180.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280: 2126–2128.

Wright, G. M., and B. Thompson. 1935. . Fauna of the national parks of the U.S. USDA Department of Interior, Washington, D.C., USA.

Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, Wyoming, USA.