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RESEARCH ARTICLE

Landscape ecology as a foundation for sustainable conservation

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Abstract Landscape ecology and conservation share a common focus on places, but they differ in their perspectives about what is important about those places, and the integration of landscape ecology into conservation is far from complete. I consider four ways in which landscape ecology can contribute to conservation. First, protected areas that are established for conservation are not stand-alone isolates. They exist in the context of broader landscape mosaics, which may encourage or discourage movements of individuals into and out of an area. Second, the landscape surroundings of a preserve may contain threats to the biodiversity within the preserve, many of them consequences of human activities. In combination, these relationships with the surroundings may make the "effective area" of a preserve different from that shown on a map. Third, the scale of an administrative area or of management action may not coincide with the scales of populations, disturbances, or ecological processes, creating challenges to both landscape ecology and conservation. Finally, landscapes encompass people and their activities; sustainability of conservation requires consideration of the tradeoffs between human uses and the biodiversity values of a landscape. I illustrate these four themes with a case study of the management of prairie dogs (*Cynomys ludovicianus*) in the Great Plains of North America, where the tensions between conservation and human land uses are particularly high. Ecologists and conservationists consider prairie dogs as keystone species in these grassland ecosystems and primary targets for conservation, but many private landowners regard them as varmints that consume valuable livestock forage and degrade rangeland condition. Effective conservation of functioning grasslands must include prairie dogs, and this in turn requires that the issues be addressed in terms of the biological, social, and cultural features of entire landscapes. Important as they are, areas protected for conservation cannot by themselves stem the tide of global biodiversity loss. The perspective must be broadened to include the landscapes where people live and work, recognizing the dynamic nature of landscapes and the factors driving land-use change. Landscape ecologists must work together to overcome the cultural differences between their disciplines, and between academic science and conservation practice and management. It can, and must, be done.

Keywords Conservation · *Cynomys ludovicianus* · Land use · Landscape context · Prairie dogs · Scale

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Introduction

Simply put, conservation is about preserving the earth's biodiversity. To "preserve" means to keep safe, to maintain. To be effective, conservation must therefore sustain populations of species, the ecosystems of which they are a part, and the habitats they need to persist and prosper. In many cases, this means protecting places for biodiversity.

Landscape ecology shares this focus on places, albeit from a different perspective. To a landscape ecologist, the places (or habitats) that so interest conservationists are elements in a larger landscape mosaic. It is the structure, spatial configuration, and context of these places, and the ways in which these influence ecological processes and undergo change, that landscape ecologists find fascinating.

The two disciplines also share a common challenge. We live in a world of burgeoning human populations, rampant development, and erosive exploitation of natural resources, all driven by the legitimate desires of people for a better life. To conservationists, the goal is to find ways to maintain biodiversity, by targeting and prioritizing places for protection or conservation management and by advocating sound environmental policies. To landscape ecologists, the goal is to use an understanding of landscape patterns and processes to design and manage land use in ways that promote the well-being of people and nature. Both aim to enhance the sustainability of landscapes, for biodiversity and for people.

There is clearly substantial overlap in the agendas of conservation and landscape ecology, and much has been written about the intersection of the two disciplines (e.g., Gutzwiller 2002; Liu and Taylor 2002; Bissonette and Storch 2003; Lindenmayer and Hobbs 2007). Yet the union is not complete. Although conservation biologists have enthusiastically embraced notions of connectivity and fragmentation (e.g., Crooks and Sanjayan 2006; Lindenmayer and Fischer 2006), many of the themes that are central to landscape ecology—scale, landscape context, boundary permeability, and the like—have yet to become common elements of conservation practice. Major investments are made to set aside places for conservation with little consideration of past and present land uses in the surrounding landscapes, much less the likely trajectories of future land-use change.

I have come to consider this intersection of conservation and landscape ecology from the perspective of decades spent as an academic scientist, first as an ecologist and then, as the discipline emerged, as a landscape ecologist. But I've also spent the past several years immersed in the world of conservation non-governmental organizations (NGOs), first with The Nature Conservancy (TNC) and now with a smaller organization, PRBO Conservation Science (formerly Point Reyes Bird Observatory). This experience has not endowed me with any great wisdom, but it has allowed me to witness first-hand the difficulties of putting the science of landscape ecology (or, indeed, any science) into conservation practice and policy.

Landscape ecology has much to offer biodiversity protection. Here I'll focus on four aspects of the linkage between landscape ecology and conservation: context, threats, scale, and sustainability. I'll address each of these in sequence and then illustrate them with a particularly challenging conservation problem. The points I make are not new—others have noted them long before me (e.g. Saunders et al. 1991)—but they bear repeating. I'll return at the end to consider how the linkage between landscape ecology and conservation might be strengthened.

Context

One of the core messages of landscape ecology is that context—the surroundings of a landscape patch or "place"—matters. How different habitats, cover types, or populations are arrayed over a landscape affects what is present and what happens at any particular place in the landscape. Much of the traditional focus of conservation, however, has been on protecting those particular places, places that have extraordinary conservation value. This approach is formalized in the notion of protected areas. These areas—nature reserves, wildlife refuges, national parks, wilderness areas, and the like—are managed primarily to maintain or restore their natural values, usually under the aegis of a government agency, land trust, or conservation organization. Worldwide, there are well over 30,000 protected areas, although "protected" has multiple meanings. The World Conservation Union (IUCN), for example, recognizes six levels of "protection," ranging from strict nature reserves and wilderness areas, managed mainly for the science of wilderness protection, to managed resource protected areas, managed primarily for the sustainable use of natural ecosystems (IUCN 1994).

A protected-area approach to conservation aligns well with the patch-matrix perspective in landscape ecology (Forman 1995). Protected areas are viewed as places (patches) that are immersed in a background (matrix) of other land covers and land uses. Although the surrounding matrix may sometimes have neutral or positive conservation value, it is usually viewed as being inimical to conservation interests. The patch-matrix view of protected areas is an expression of an old (and, in my view, outmoded; Wiens 1994; Opdam and Wiens 2002) belief that nature reserves can be thought of as islands and that island biogeography theory therefore provides valuable insights about the design of reserves (MacArthur and Wilson 1967; Shafer 1990). As conservation planning has evolved to consider suites of protected areas derived by increasingly sophisticated reserve-selection algorithms (Pressey and Cowling 2001; Groves 2003; Margules and Sarkar 2007), attention has shifted from individual reserves to sets of reserves that make complementary contributions to the protection of regional biodiversity. But too often the reserves are regarded as patches in an inhospitable or featureless matrix. A good deal of conservation is carried out in highly fragmented landscapes where the patches with high conservation value are often surrounded by a sea of human uses, so it is not surprising that this patch-matrix approach to protected areas has persisted in conservation.

But this approach is incomplete and shortsighted. Landscape ecology tells us that the "matrix" is far from uniform and not all places in it are lacking in conservation value. Landscapes are mosaics of places with different vegetation cover, ecological communities, and land uses. These places, be they sharply bounded landscape elements ("patches") or areas that grade into one another over gradients or ecotones ("fuzzy patches"), are interconnected both structurally and functionally. Decades ago, Aldo Leopold drew attention to the value of the interspersion of varied land uses, habitats, and edge effects in landscapes to wildlife populations (Leopold 1933). More recently, this relationship has been cast in terms of the ways in which landscape heterogeneity can enhance plant and animal species diversity (β-diversity) beyond that found within individual habitat patches (α-diversity) (Rosenzweig 1995). Increasing attention is being given to the connectivity among places in a landscape (Crooks and Sanjayan 2006) and to linking conservation areas together in ecological networks (e.g. Jongman and Pungetti 2004). The linkages among core conservation areas, corridors, buffer areas surrounding the core areas, and sustainable use areas have been recognized in a multinational program, the Pan-European Ecological Network (PEEN) (Bonnin et al. 2007; http://www.countdown2010.net/archive/paneuropean.html). Functionally, individuals and populations within a protected area may not recognize the jurisdiction or fence line demarking the boundary of the preserve as an impermeable barrier, but instead may roam well beyond the boundary to use resources, seek mating opportunities, and the like. Dispersal of individuals from a designated area (e.g., a breeding area or a population "source"; Pulliam 1988) to other breeding locations (or population "sinks") affects the genetic and demographic structure of populations. Although evolutionary and population biologists often tend to think of dispersal only in terms of the sources and ending locations for dispersers (see, e.g., the contributions to Clobert et al. 2001), the probability of individuals dispersing from one location to another may have as much to do with the structure and composition of the surrounding landscape mosaic as with conditions within the source or target areas (Fig. 1) (Wiens 2001).

The interactions and interdependencies between individuals and populations within a protected area or landscape patch and the surrounding landscape mosaic have the consequence of altering the "effective area" of a protected area. Movement into the surrounding landscape creates a larger functional area than that depicted on a map of administrative, ownership, or management units (Fig. 1a). The efforts of conservation planners and land managers to achieve their conservation aims may miss the target if they are focused only on protected areas without considering functional linkages with the surrounding landscape. The consequences may be especially troublesome if the protected area is small relative to the scales within which the populations or species of conservation interest operate (see below).

Threats

Conservation planning usually includes a consideration of the factors that threaten the persistence of the

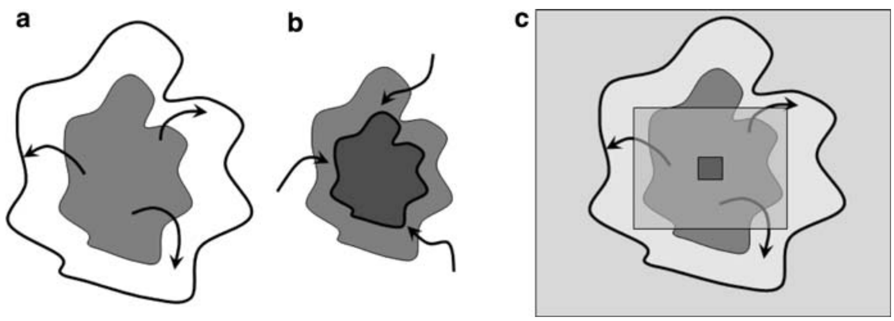

Fig. 1 Influence of (**a**) movements of conservation targets (e.g., individuals of key species) from within a protected area into the surrounding landscape, or (**b**) movements of potential threats (e.g., predators, competitors, invasive species) from the surrounding landscape into a protected area on the "effective area" of the protected area. The protected area is shown in medium gray. In (**a**) the effective area is shown by the dark line; in (**b**) by the dark gray area within the protected area. Panel (**c**) illustrates the effects of different scales of conservation planning or management (rectangles) in relation to the size of the effective area shown in (**a**)

biodiversity within a protected area as well as the conservation targets that represent that biodiversity or are of special concern (e.g., threatened or endangered species, community types) (Groves 2003). More often than not, these threats come from beyond the boundaries of a protected area—from the surrounding landscape. When Janzen (1983) observed that "no park is an island," he was thinking particularly of predators that lurk in the surrounding habitats that enjoy feasting on the biodiversity within a park. Increasingly, however, the threats are created by human activities that convert the surroundings to agricultural monocultures or housing developments, often with new suites of predators, pathogens, and invasive species that threaten the sanctity of the preserve. Of 124 conservation project plans by The Nature Conservancy, for example, 61% listed development as a primary threat to biodiversity, while 37% indicated that fragmentation and isolation of the area were major threats. In their unified classification of direct threats to biodiversity targets, IUCN and the Conservation Measures Partnership (IUCN-CMP 2006) list some 46 categories of threats. Although some of these (e.g., hunting, logging, recreation) may occur within a protected area, many are generated in the surrounding landscape and affect populations and ecological communities inside the preserve. Collectively, these external threats may act to reduce the "effective area" of a preserve to something considerably less than that depicted on a map (Fig. 1b). Indeed, one reason why small preserves are often thought to have limited conservation value is because there is no core area that is immune from these external threats.

To do effective conservation planning, it is necessary to move beyond categorizations of threats as internal or external and instead deal with the specifics. For example, how does the composition and structure of the landscape surrounding a protected area affect the probability that a given threat will in fact affect the conservation targets within a protected area? This probability will be determined by a large variety of factors—the location or source of the threat, its movement or transmission potential, the permeability of different elements in a landscape to spread of the threat, the configuration of the landscape relative to the protected area, the sharpness and permeability of the boundary of the preserve, and so on. These aspects of landscape structure and function and patch-boundary characteristics are central to much of what landscape ecology does.

Scale

One of the signature accomplishments of landscape ecology has been to draw attention to the importance of spatial scale. Scale influences both the form of ecological patterns and processes and our perception of those patterns and processes (Wiens 1989; Peterson and Parker 1998; Wu et al. 2006). The biodiversity that conservationists strive to preserve contains elements that operate at quite different scales from one another. It is trite to observe that beetles, birds, and bison relate to a grassland environment at vastly different scales. Yet a grassland area designated for conservation that adequately captures the living requirements of some organisms may fail to meet the requirements of others. Conservation of multiple targets requires management that is matched to the multiple spatial scales of those targets (Turner et al. 2002).

There is a certain irrefutable logic to the notion that the larger a preserve, the greater the range of scales of the critical components of biodiversity will be included, and the mantra of conservation has long been that "bigger is better." But this is a view derived, at least in part, from the classic species–area relationship in ecology and a simple "preserves-as-islands" perspective, in both of which size alone is usually the critical consideration. Size, however, is contingent on context. A forest preserve of a given size embedded in a larger expanse of forested habitat is likely to have a different conservation value than that of an area of the same size surrounded by a landscape fragmented by agriculture or development. As noted above, these structural relationships may be altered by the functional linkages and interactions (both positive and negative) between a preserve and its surroundings (Fig. 1). The functional scale of a preserve is influenced by its landscape context. So it is not simply that landscape ecology calls attention to the importance of scale in conservation; instead, the characteristics of the landscapes themselves influence the scale(s) on which conservation and management must be conducted. A consideration of protected areas absent a consideration of scale is likely to be incomplete (Fig. 1c).

Sustainability

Moving beyond a patch-matrix approach to protected areas to a perspective that acknowledges and incorporates the heterogeneity of the landscape mosaics in which such areas are embedded involves more than a recognition that context, external threats, and scale are important. The places beyond the boundaries of protected areas are often the places where people live and work, where human activities create and alter the landscape (Turner et al. 1990; Nassauer 1997; Miller and Hobbs 2002). More often than not, these are regarded as the places where people and biodiversity come into conflict. Human uses of the landscape are considered as threats to biodiversity. Indeed, habitat loss and fragmentation due to human land uses are widely deemed to be the preeminent causes of declining species populations and biodiversity loss (Wilcove et al. 1998). This, of course, is a driving force behind the efforts to set aside places as nature reserves and protected areas.

Instead of adopting a "circle the wagons" approach that views places as "protected" or "not protected" (and therefore of little conservation value), conservation would be better served by recognizing that land uses are arrayed across a spectrum of differing intensities of use and potential impacts on biodiversity. In terms of conservation, a landscape may better be depicted as a mosaic of shades of gray rather than in stark black-and-white (Wiens 2007a). In general, we expect the capacity of places in the landscape to support native biodiversity in a sustainable fashion to decline as the intensity of human use of those places increases (although not necessarily in the linear fashion shown in Fig. 2). There is likely to be some threshold of increasing land-use intensity where the biodiversity value falls below a level that will maintain viable populations of key species, functioning natural ecosystems, or other conservation objectives. This is the *biodiversity value* threshold. On the other hand, society may be willing to accept further diminishment in the conservation value of a landscape in the interests of increased intensity of human use. Land-use decisions are usually driven more by economics than by biodiversity. This is the *societal value* threshold. There is variation around both of these thresholds, of course. The biodiversity value threshold may higher (i.e., tolerant of less intense human land-use), for example, where threatened or endangered species are concerned. The societal value threshold may be closer to the biodiversity value threshold where the land uses that favor biodiversity also provide critical ecosystem services to people. Forested watersheds that provide clean water or native habitats that foster pollinators important to agricultural crops are examples.

Opposing forces tend to move these thresholds in opposite directions (Fig. 2). Economic forces and incentives may pull the societal value threshold toward increasing use intensity, further diminishing conservation value. On the other hand, the objective of most conservation work is to enhance biodiversity

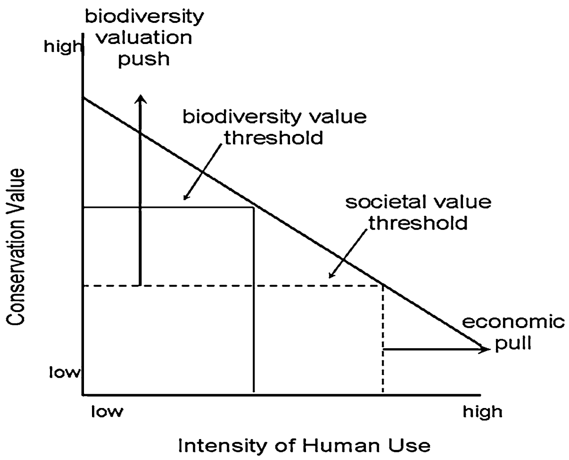

Fig. 2 The relationship between the intensity of human use of an area or landscape and the conservation value (biodiversity protection) of that area or landscape. For simplicity, the relationship is shown as a linear decrease in conservation value with increasing intensity of human use, although it is probably a nonlinear relationship. If one is interested in the protection of biodiversity, only a certain level of human use can be accepted before the diminishment of conservation value is too great (the biodiversity value threshold). If one's interest is in human use of the landscape, a greater intensity of human use may be desired, with a correspondingly greater loss of conservation value (the societal value threshold). An emphasis on economics pulls the societal value threshold toward more intense human use, whereas an emphasis on conservation pushes the biodiversity value threshold toward greater conservation value, with reduced human use

value by setting aside protected areas, restoring habitat, or undertaking ecologically sound resource management. These efforts push the biodiversity threshold higher by reducing the intensity of human land use.

This push–pull tension embodies the inherent polarization of the extremes of pure environmentalism and unbridled economic development. For conservation to be a sustainable endeavor, however, it must occupy the "radical middle," balancing the environment and biodiversity with economics and human well-being (Millennium Ecosystem Assessment 2005). Recognition by conservationists that many human land uses can be compatible with conservation goals may help to broaden this middle by abating the strength of the biodiversity push. At the opposite extreme, the growing appreciation that functioning natural ecosystems provide manifold goods and services to people and that these benefits have real economic values (Daily and Ellison 2002; Millennium Ecosystem Assessment 2005) may help to redirect at least some of the economic pull back toward the middle. Not coincidentally, this "middle" is where, on the ground, landscapes are neither all protected nor all developed, but are the richly textured mosaics on which landscape ecologists have lavished their attention.

These propositions may seem theoretical and abstract. To make them more concrete and tangible, it may help to consider a very real, and very contentious, conservation challenge, one in which it is essential to adopt a landscape perspective.

A case study: Prairie dog conservation in the North American Great plains

Black-tailed prairie dogs (*Cynomys ludovicianus*) are medium-sized, highly social, burrowing mammals that live in dense colonies ("towns") or colony complexes (Hoogland 2006). Two centuries ago, they were one of the most abundant and ubiquitous mammals in grassland ecosystems of the North American Great Plains. As a result of widespread habitat conversion and loss, eradication efforts, and disease, populations are now less than 2% of these former levels and the species is an important target of conservation efforts. Prairie dogs are a focus of conservation concern not only because their abundance has been so dramatically altered, but also because their colonies host a variety of associated species—burrowing owls (*Athene cunicularia*), prairie rattlesnakes (*Crotalis viridis*), and black-footed ferrets (*Mustela nigripes*) as well as several other vertebrate and invertebrate species. They are considered to be keystone species in these ecosystems (Kotliar 2000). Because prairie dogs graze the vegetation within a colony to a lawn-like stature, however, they may also alter the composition of the plant community and destroy habitat that may be essential for other conservation targets (e.g., lesser prairie-chickens, *Tympanuchus pallidicinctus*). The needs of prairie dogs must be balanced with those of other conservation priorities.

Recognition of the ecological and conservation importance of prairie dogs is not shared by all members of society. Within the range of prairie dogs, many private landowners regard them as "varmints" that degrade rangeland condition and consume forage that could support domestic livestock. Landowners who allow prairie dogs on their properties are often stigmatized as poor managers who permit colonies to grow to the point where range condition is damaged and neighboring properties may be affected. In some situations, landowners may be legally obligated to control prairie dogs on their property.

So the push–pull tensions of conservation in a socially contentious climate are very much in evidence. Federal agencies and conservation non-governmental organizations (NGOs) such as The Nature Conservancy manage designated areas to protect and enhance prairie-dog colonies and colony complexes. When protected from control efforts or excessive disturbance, prairie-dog populations are capable of astonishing growth, especially in areas not susceptible to plague (see below). At TNC's 6,760-ha Smoky Valley Ranch Preserve in Kansas, for example, the area occupied by prairie dog colonies increased from 104 ha when the ranch was purchased by TNC in 1999 to over 1,400 ha in 2006, an increase in estimated prairie dog abundance from 4,000 to over 55,000 in 7 years (R. Manes, personal communication). As colonies grow and animals disperse, however, they may cross the boundaries of protected areas and enter private lands where ranching is often the primary land use, fostering resentment and demands to control or eradicate colonies. Prairie-dog conservation and management cannot succeed in the long term by focusing exclusively on protected areas; the solutions, both ecologically and sociologically, require a landscape perspective. How do the four themes of landscape ecology I discussed earlier relate to prairie-dog conservation?

Context

The National Grasslands, TNC preserves, or other areas that are managed to maintain or enhance prairie dog populations do not exist in isolation from their surroundings. In most areas, the landscape is a mosaic of public and private ownership with varied land uses (Fig. 3). Given the intensity of land use in the landscape and the distain of some landowners for prairie dogs, it may be tempting to apply the island model to protected areas and to focus management

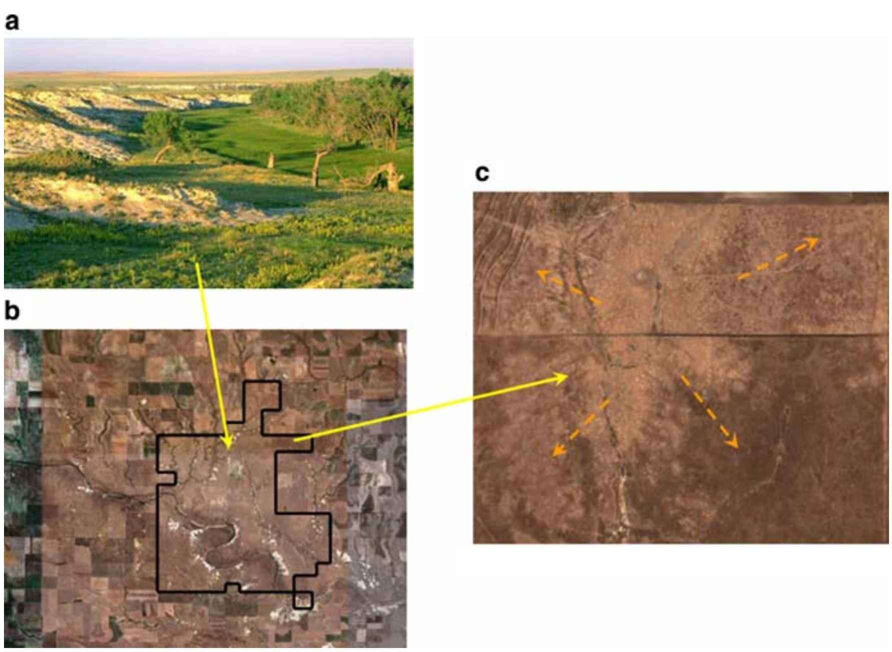

Fig. 3 (**a**) The Smoky Valley Ranch Preserve of The Nature Conservancy in western Kansas. The GoogleEarth image (**b**) illustrates the fragmented nature of the surrounding landscape, which is used primarily for ranching and dryland agriculture; all of the surrounding area is in private ownership. A prairie dog colony in the northeastern part of the preserve (**c**) is one of a larger complex of colonies on the preserve. This colony straddles the boundary between the preserve and private land; the dashed arrows illustrate potential dispersal from the core colony area and colony expansion. The location of the Preserve in the Great Plains is shown in Fig. 4

Fig. 4 Range of the black-tailed prairie dog in the Great Plains of North America. Sylvatic plague occurs west of the bold line, whereas colonies located east of the line are (for now) free of plague. The dark circle shows the location of the Smoky Valley Ranch Preserve

efforts within the preserves. The high growth potential of populations within protected areas, however, promotes dispersal of individuals. Some of these emigrants establish new colonies as part of a larger colony complex within the protected area, but others move beyond the preserve boundaries into the surrounding landscape, creating conflicts with adjacent landowners. Where natural boundaries (e.g., topography, streams, tall dense vegetation) exist, such movements may be restricted. Often, however, the lands beyond the boundaries are attractive to prairie dogs, especially in rangelands subjected to heavy grazing or during drought. The dispersal pathways of prairie dogs, and therefore the probabilities that they will establish colonies on properties where they are not wanted, depends on conditions within the preserve (e.g., colony size and density), permeability of the boundary to movements, and the configuration of landscape elements with different habitat suitabilities and permeabilities in relation to the preserve boundaries (Wiens et al. 1993). If managers are to target prairie-dog control efforts (which may be necessary in some circumstances) where they will be most effective, an understanding of these elements of the landscape context of a protected areas is essential.

Threats

The growth and expansion of prairie dog colonies at Smoky Valley Ranch suggest that threats to populations within managed preserves may be minimal. Predation does occur, but one natural predator, the black-footed ferret, is recovering from near-extinction and only occurs in a few locations and the effectiveness of other predators (e.g. ferruginous hawks, *Buteo regalis*) is blunted by the social dynamics and alarm-calling of prairie dogs within colonies (Hoogland 2006).

In the western two-thirds of the prairie dog's range, however, it is subject to sylvatic plague epizootics (Antolin et al. 2002; Stapp et al. 2004). The plague bacterium (*Yersinia pestis*) is carried by fleas that occupy burrows and infest prairie dogs. Prairie dogs have little resistance to the bacterium, so when a colony is exposed to plague and an epizootic ensues, almost all individuals in a colony die. It may be several years before the colony is re-established by individuals dispersing from other colonies. In areas where plague occurs, then, colony dynamics may be largely determined by the incidence of plague. In large preserves in which several colonies are linked together in a colony complex, re-establishment of a colony that has suffered plague may occur from elsewhere in the preserve, but in smaller preserves both the initial occurrence of plague and the subsequent re-establishment of colonies come from the surrounding landscape. How other colonies are distributed through that landscape, and the permeability of the landscape to dispersing prairie dogs (or other flea hosts), may be major determinants of the probability that a given colony will be exposed to plague or later re-established.

The susceptibility of prairie dog colonies to plague also affects public perceptions of the value of prairie dogs and their conservation. The plague bacterium that affects prairie dogs also causes plague in humans (it killed millions of people in Europe in the Middle Ages—the "black death"). At colonies located in close proximity to urban and suburban developments, domestic pets may bring infected fleas from the prairie dog towns into households. Public health concerns may foster calls for treatment of the colonies to control fleas, programs to capture and transport prairie dogs to more distant locations (which is illegal in some areas), or the eradication of entire colonies.

Scale

Clearly, the size of a protected area is important to prairie-dog management. A small preserve (say, 10 s of ha) may only be capable of supporting a small colony and dispersing individuals will be likely to move into areas outside the preserve, where they may generate landowner reactions that make conservation efforts more difficult. Conserving colony complexes, in which the bulk of dispersal may be among individual colonies in the complex, requires that considerably larger areas be protected. If the aim is to re-introduce black-footed ferrets as part of restoring functional grassland ecosystems, a much as 800 ha of occupied prairie-dog habitat may be needed to establish a "nursery" population of ferrets (J. Lockhart, personal communication).

The scale of conservation is particularly important in areas subject to plague. There the typical scenario is for colonies to become established, grow, and produce emigrants, eventually to be infected by plague and die out, only to repeat the cycle later on. Over a broad landscape there is a shifting pattern of colonies winking into and out of existence, their dynamics driven by plague, the biology of the fleas, and dispersal of both the prairie dogs and the fleas. At a given time, some colonies serve as sources and others as sinks in a classic metapopulation structure (Stapp et al. 2004), with the "sourceness" or "sinkness" of any one colony depending on its phase in the plague cycle. Managing at the scale of a single colony or protected area (especially a small one) will miss these broader scale spatial dynamics and is likely to result in ineffective conservation.

Sustainability

In many respects, understanding prairie-dog dispersal is the key to their conservation. Small, isolated colonies generally cannot persist alone, but must be part of a broader network of sites linked together by dispersal, especially in areas where plague is prevalent. Managing dispersal therefore requires a consideration of landscape composition and structure. In areas of the grasslands where ranching is the primary land use there may be few impediments (except for angry ranchers) to dispersing individuals. In landscapes with more varied land uses, however, the fragmented mix of grasslands, croplands and suburban development can present a perilous maze to an emigrant prairie dog. Unfortunately, we know little about the habitat preferences of prairie dogs during dispersal, so it is difficult to design a landscape that will facilitate or direct dispersal (Antolin et al. 2006).

Prairie-dog conservation is a contentious issue because prairie dogs inhabit a mosaic of public, conservation, and private lands. The stakeholders in these landscapes have dramatically different perspectives about the value of prairie dogs or the need for conservation. Sustainable conservation of prairie dogs, and of the grassland ecosystems in which they occur, will require that these perspectives be taken into account. In particular, the view that prairie dogs are bad stems in part from a perception of what "good" or "healthy" rangeland should look like. The degraded appearance of a dense prairie-dog town simply does not fit with this image (especially during drought conditions). But there also may be very real economic costs to pastoralists from the loss of potential livestock forage to prairie dogs. Some estimates of economic losses in livestock production associated with prairie dogs have been made (Hygnstrom and Virchow 1994; Derner et al. 2006), but more rigorous and comprehensive quantification of the real economic costs (and benefits) of prairie dog colonies of different sizes under a range of ecological, climatological, and market conditions is needed. Such an assessment should be the foundation of incentive programs implemented to reward landowners for including their lands in grassland conservation networks. Because the role of particular landholdings in broad-scale prairie-dog dynamics and conservation is contingent on landscape configuration as well as land use, such analyses should be spatially explicit.

In many ways, the structure and composition of rangelands in the western Great Plains are compatible with both the conservation of prairie-dog populations that are viable and persist at a metapopulation scale, and with a ranching economy and way of life that are also viable and persist. Maintenance of these rangelands as working ranches can represent a “win-win” situation (Rosenzweig 2003) that is far preferable to conversion of these landscapes to development or agriculture (Knight et al. 2002).

Concluding discussion

As human populations grow and economies expand, fewer and fewer places are left for nature. Indeed, there are probably no places on earth free of the footprint of humanity—“nature” has been domesticated (Sanderson et al. 2002; Kareiva et al. 2007; but see Wiens 2007b). The need to protect those places where biodiversity still retains some elements of its naturalness and functionality is increasingly urgent.

Important as they are, however, protected areas by themselves cannot stem the tide of global biodiversity loss. The perspective must be expanded to encompass entire landscape mosaics that include not only the protected areas but other places with different land cover, human uses, and conservation values. The characteristics of this mosaic may enhance the value of a preserve by providing resources that supplement those within the preserve or may contain threats that influence the sanctity of the preserve. In no case, however, can a preserve be considered in isolation from the surrounding landscape.

Thinking of a protected area or preserve in this way, however, makes it too easy to slip into a simplistic patch-matrix conceptualization of landscapes. Conservationists must recognize that the variety of land covers and human uses in a landscape represents a range of potential conservation values and that landscape design can contribute to realizing or enhancing these values. Landscape ecologists can help by quantifying and mapping these values and the tradeoffs between conservation value and human uses and documenting how alternative spatial arrangements of landscapes influence ecological flows and the conservation value of the landscape as a whole.

All of this, of course, is complicated by landscape change. Conservation planners often target places for protection based on current criteria—size, occurrence of critical conservation targets, ownership, cost, proximity to other protected areas. But landscapes are dynamic. Land uses change, increasingly driven by changes in global economics (witness the rise of biofuels). With these changes, land cover, the distributions of plants and animals, and conservation values also change. Because of the spatial interdependencies among places in a landscape, exactly how these changes play out will depend on the configuration and composition of a landscape. All of this makes it difficult to predict the trajectory of change in the landscape milieu in which a protected area is embedded.

And then, of course, there is climate change. During droughts, for example, the dispersal of prairie dogs into lands adjacent to colonies changes. This is when livestock production and ranching economics may be pushed to the edge, so the reactions of landowners to such transgressions also change. Current climate-change models predict warmer and drier summer conditions and an increase in extreme events for much of the Great Plains (D. Ojima, B. Baker, personal communications). These conditions may favor prairie dogs but exacerbate their interactions with ranchers, especially if droughts become more frequent. More broadly, shifts in species distributions and plant communities are anticipated (and are already occurring) in many regions of the world (e.g., Lawler et al. 2006; Prasad et al. 2007; Matthews et al. 2007; Sekercioglu et al. 2008). Combined with changes in global economies and agriculture, these distributional shifts will alter the landscape context of even the most remote protected areas. Conservation and landscape ecology must integrate the work of climate-change scientists into their shared agenda.

Conservation has been called a “crisis discipline” because so often the focus is on protecting species that teeter on the brink of extinction. Yet in the broader sense conservation is about preserving the full range of the earth’s biodiversity—*preserving*, not just protecting. Making conservation sustainable requires casting it in a landscape context, incorporating the places where people live and work as well as those places under protection, and doing so in a way that considers landscape changes over time. This will compel conservationists to work with sociologists, land-use planners, economists, *and* landscape ecologists to understand the factors that drive land use and land-use change at landscape, regional, and global scales and to define when and where those human actions are compatible with biodiversity conservation and when and where they are not. The growing recognition that biodiversity provides people with values that go far beyond aesthetics, spirituality, or recreation to encompass a range of ecosystem services means that the sustainability of cities, villages, and cultures is linked with the sustainability of natural ecosystems. Landscape ecology provides a framework in which to develop this shared sustainability.

So why haven't landscape ecology and conservation become more fully integrated? There are several reasons (Wiens 2007c). First, landscape ecologists and conservationists have different goals. Landscape ecologists aim to understand the causes and consequences of spatial heterogeneity of landscapes, while (put simply) conservationists focus on preserving species and biodiversity and tend to lump all that heterogeneity into "habitat." Second, landscape ecologists and conservationists tend to work and think at different scales. Although the size of protected areas is becoming larger, many are still on the order of a few hectares to several square kilometers. Land ownership, which often determines conservation actions and management, typically occurs over a similar range of scales. A good deal of landscape ecology falls within this range, although landscape experiments are usually conducted at finer spatial scales, whereas many land-cover analyses are conducted at much broader scales. Integrating data and concepts from different scales remains a formidable challenge.

Third, both landscape ecology and conservation are affected by a gap between science and practice. Much of the knowledge, data, and analyses that form the empirical and theoretical foundations of both disciplines is generated in an academic culture. In principle, this information and knowledge should flow seamlessly into applications in landscape management and biodiversity conservation, but they don't, at least as much as they should. The emphasis in an academic culture is on research, and the reward system is based on publishing and obtaining grant funding. In landscape management and conservation practice, the emphasis is on actions that will produce quick results. In my experience, managers and practitioners *want* to base their actions on good science but have neither the time to wait for science to produce acceptably certain (i.e., $P < 0.05$) answers nor the training to extract the important nuggets from dense scientific papers. Academic scientists *want* their findings to have an impact on management, but they are understandably reluctant to abandon the nuances of complex studies to provide simple messages to managers, and they often lack the communication skills to do so.

The barriers to bridging the gap between science and practice and achieving a closer integration of landscape ecology and conservation are not great. We know what the conceptual issues are, and we know where landscape ecology can help conservation move out of the preserves into the landscape. The barriers are largely cultural, embedded in the histories and paradigms of the two disciplines. We need to reach across the cultural differences to work together in the substantial space of our shared perspectives. If landscape ecology is truly a transdisciplinary science (Naveh 2005), it should be easy.

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