Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks

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Approaches to conservation and natural resource management are maturing rapidly in response to changing perceptions of biodiversity and ecological systems. In past decades, biodiversity was viewed largely in terms of species richness, and the ecosystems supporting these species were seen as static and predictable (Fiedler et al. 1997). Conservation activities were often aimed at hotspots rich in total species or in rare species (Noss 1987). Consequently, relatively small nature preserves proliferated through the 1970s and 1980s, as did endangered species management and recovery plans on more extensive public lands.

More recently, biodiversity is being viewed more expansively, to include genes, species, populations, communities, ecosystems, and landscapes, with each level of biological organization exhibiting characteristic and complex composition, structure, and function (Noss 1990). As a result, current recommendations for biodiversity conservation focus on the need to conserve dynamic, multiscale ecological patterns and processes that sustain the full complement of biota and their supporting natural systems (e.g., Angermeier and Karr 1994, Turner et al. 1995, Harris et al. 1996, Poff et al. 1997).

Translating expanding perceptions into pragmatic guidelines and appropriate action is a challenge for conservation organizations and natural resource agencies. In this article, we describe an imperfect but practical framework that can help practitioners transition from biodiversity conservation based on rare or endangered species to conservation based on ecosystem- and landscape-level concepts. We begin by providing a brief overview of the scientific concepts from which the framework has evolved. We then describe a convenient way to categorize ecosystems and species based on spatial pattern and scale. Next, we describe three types of "functional conservation areas"—sites, landscapes, and networks—defined by the scale of the ecosystems and species they are designed to conserve. We then present a suite of ecological attributes that can be used to evaluate the functionality or integrity of a conservation area at any scale. Finally, we discuss the challenges of implementing these ideas in applied settings. We illustrate concepts with examples and a case study from the work of The Nature Conservancy (TNC), a nongovernmental organization dedicated to conserving biodiversity throughout the United States and in selected other countries worldwide (TNC 1996).

A FRAMEWORK FOR BIODIVERSITY CONSERVATION BASED ON MAINTAINING FOCAL ECOSYSTEMS, SPECIES, AND SUPPORTING NATURAL PROCESSES WITHIN THEIR NATURAL RANGES OF VARIABILITY

The science of conservation biology

The science of conservation biology has evolved from a crisis-oriented discipline focused on rare or endangered vertebrates to a more proactive experimental discipline focused on patterns and processes at multiple scales. Early on, the technique of population viability analysis was developed to estimate the minimum population size necessary for a particular rare species to persist over time (Ruggiero et al. 1994). Results from these analyses could rarely be validated, and the analyses themselves were information, time, and resource intensive. They quickly illuminated the inefficiency and reductionism inherent in rare- or single-species approaches (Franklin 1993).

Consequently, the single-species approach to conservation quickly broadened to encompass groups of species and certain individual species (e.g., so-called umbrella species, whose habitat requirements are believed to loosely encapsulate an array of additional species; Launer and Murphy 1994). For instance, protecting mammals with large area requirements and diverse habitat needs may

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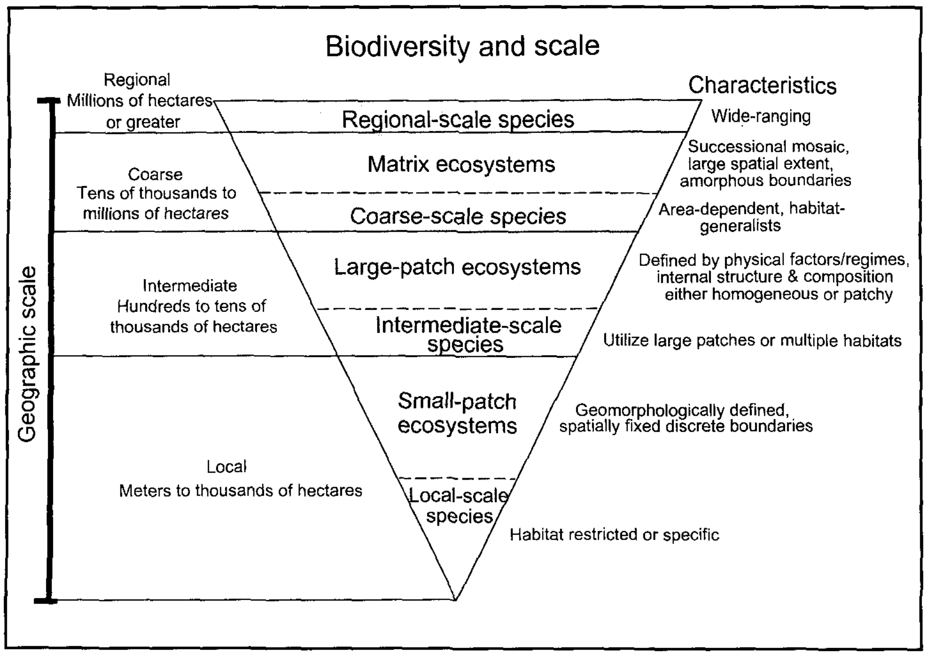


Figure 1. Biodiversity at various spatial scales. Levels of biological organization include ecosystems and species. Ecosystems and species are defined at four geographic scales, including local, intermediate, coarse, and regional. The general range in hectares for each spatial scale is indicated (left of pyramid), as are common characteristics of ecosystems and species at each of the spatial scales (right of pyramid).

protect species with smaller area requirements and more specific habitat needs (Berger 1997). Species guilds—groupings of species based on specific characteristics (e.g., foraging behavior)—is another multispecies approach to conservation and management (Block et al. 1995).

Species guild and umbrella species approaches were a substantial improvement over single-species approaches, but their use in conservation planning still had significant limitations. First, at the site scale, populations of different species typically vary and fluctuate in complicated ways (e.g., one interior forest species may decline while another increases). Second, sites conserved and managed for the needs of a particular species or even a small group of species may fail to conserve other critical components of the ecosystem, including other species or processes that substantially influence the species of concern (Morrison 1986, Block et al. 1987, Landres et al. 1988). Considering that vascular plants and vertebrates together make up less than 10% of known biodiversity, any particular set of species is an extremely small fraction of the biota at any one place (Franklin 1993). Thus, a growing appreciation of the enormous complexity and dynamic nature of ecological systems led to the concept of ecosystem management, wherein success is best assured by conserving and managing the ecosystem as a whole (Christensen et al. 1996).

The shift in focus from species to ecosystems generated new questions. For example, how are ecosystems defined and delineated? How can it be determined whether a particular ecosystem has ecological integrity (i.e., the ability to maintain component species and processes over long time frames)? Ironically, the latter question prompted managers to again assess individual species, but this time as indicators. Indicator species are those used to index or represent environmental conditions, particularly conditions related to ecological degradation (Cairns et al. 1993).

In addition, attempts to unify species- and ecosystem-level concepts in biodiversity conservation prompted the so-called coarse filter–fine filter strategy. This strategy stresses the importance of conserving intact examples of all communities or ecosystems to protect the vast majority of species. Any rare or specialized species that would likely go unprotected under a coarse-level approach are treated individually (i.e., the fine filter; Noss 1987, Hunter 1991).

New ecosystem-oriented paradigms stress that natural systems are vastly complex assemblages of species with elaborate internal and external ecological processes and interactions that help maintain the entire system (Noss et al. 1997). Ecological processes include decomposition, nitrogen cycling, pollination, seed dispersal, energy capture, food webs, insect outbreaks, disease, herbivory, and predation. Some species—including top-level carnivores (Paine 1974), dominant herbivores (Naiman 1988), and builders such as beaver, prairie dog, or gopher tortoise (Perry 1994)—may be disproportionately important in maintaining these critical processes, and the removal of such "keystone" species may have a cascade effect on other species and processes.

Another important concept that has emerged in conservation biology and ecology over the last several decades is that of the metapopulation—a group of subpopulations linked together by dispersal of individuals and gene flow. Metapopulations are often characterized by sources and sinks. Sources consist of suitable or optimal habitat and generally produce excess individuals, and sinks are composed of unsuitable habitat, in which population size cannot be maintained without immigration from source areas. Pulliam (1988) demonstrated that as little as 10% of a population may be located in source habitats and still be responsible for maintaining 90% of the population found in sink habitats.

Biodiversity and spatial scale

Scientists and practitioners have long recognized that biodiversity exists at many levels of biological organization, from genes to landscapes (Noss 1990, Angermeier and Karr 1994). In this article, we focus on two levels of biological organization: ecosystems and species (we assume that focusing efforts at these levels will also conserve genetic- and landscape-level diversity). We define ecosystems as dynamic assemblages or complexes of plant and/or animal species (including vascular and nonvascular plants, vertebrates, invertebrates, fungi, and microorganisms) that occur together on the landscape; that are linked by similar ecological processes (e.g., fire, hydrology), underlying environmental features (e.g., soils, geology), or environmental gradients (e.g., elevation); and that form a cohesive and distinguishable unit.

Biodiversity also occurs at a variety of spatial or geographic scales. Our framework distinguishes ecosystems and species at four geographic scales: local, intermediate, coarse, and regional. Species in the framework occur at all four spatial scales (Figure 1). Ecosystems occur at three of the four scales and are described in relation to their spatial patterning (i.e., small-patch ecosystems at the local scale, large-patch ecosystems at the intermediate scale, matrix ecosystems at the coarse scale; Figure 1). Specific conservation areas generally contain ecosystems and species at multiple spatial scales that nest together in complex configurations.

Local geographic scale. Both small-patch ecosystems and local-scale species exist at a local geographic scale (i.e., meters to thousands of hectares). Local-scale species are restricted to a particular habitat, are immobile or poor dispersers, and include many species of invertebrates and plants. For example, the Bay checkerspot butterfly (*Euphydryas editha bayensis*) is a relatively poor disperser that is restricted to serpentine grasslands in California (Murphy and Weiss 1988). Small-patch ecosystems tend to be relatively discrete, geomorphologically defined, and spatially fixed; they often occur because of distinct abiotic factors (e.g., geologic outcrops, unique soils, or hydrologic features, such as seeps). Local-scale species are usually closely connected with specific small-patch ecosystems. Typical examples of small-patch ecosystems in an eastern deciduous forest landscape include calcareous fens, acidic bogs, and high-elevation rocky summits (Anderson et al. 1998). Examples in the western United States include cienega wetlands, desert spring pools, serpentine grasslands, and fern grottos supported on cliff faces by groundwater seeps.

Intermediate geographic scale. Both large-patch ecosystems and intermediate-scale species exist at an intermediate geographic scale (i.e., hundreds to tens of thousands of hectares). Large-patch ecosystems are relatively discrete, defined by distinct physical factors and environmental regimes, and are significantly larger than small-patch ecosystems. Some large-patch ecosystems—such as red maple swamps, coastal salt marshes, and redwood forests—are defined by relatively stable physical factors and tend to be fairly uniform in internal composition and structure. Other large-patch types, such as western riparian ecosystems, northeastern pine barrens, prairie savanna mosaics, and aquatic macrohabitats in rivers, are defined by dynamic and more frequent disturbance regimes. These large-patch ecosystems are variable in structure and composition, with distinctly different internal habitat types and seral stages that shift and rearrange over time and space. We refer to these dynamic habitat types and seral stages within large-patch ecosystems as "patch types." Small- and large-patch ecosystems commonly make up the majority of coarse-filter diversity in any given region.

Intermediate-scale species depend on large-patch ecosystems or on multiple habitats. For example, a floodplain-spawning fish uses the main channel, floodplain backwaters, and sloughs of aquatic ecosystems. Another example is decurrent false aster (*Boltonia decurrens*), an imperiled floodplain plant that occurs only along the Illinois River and at its confluence with the Mississippi River. *B. decurrens* depends entirely on a dynamic large-patch floodplain ecosystem and germinates on exposed mudflats created by spring floods (Smith et al. 1993). Even though *B. decurrens* inhabits a single patch type (exposed mudflats), we consider it an intermediate-scale species because this habitat is part of a large-patch riparian mosaic.

Coarse geographic scale. Matrix ecosystems and coarse-scale species occur at geographic scales of tens of thousands to millions of hectares. Terrestrial ecosystems at this scale include the dominant (or historically dominant) matrix-forming vegetation in which large- and small-patch ecosystems are embedded. In the Northeast, matrix ecosystems consist of spruce–fir forests, northern hardwood forests, and their successional stages (Anderson et al. 1998). In the southeastern Atlantic Coastal Plain, longleaf pine (*Pinus palustris*) forests historically dominated a vast portion of the landscape. In the West, various types of sagebrush scrub (*Artemisia* spp.) and grasslands form an extensive matrix in low-elevation intermountain areas. Matrix ecosystems are nondiscrete in their boundaries and are defined by general, widespread climatic and elevation gradients.

Species at the coarse scale are habitat generalists, moving among and using ecosystems at multiple scales. Greater prairie chickens (*Tympanuchus cupido pinnatus*) of the central Great Plains are a coarse-scale, area-dependent species. They depend on large areas of the historic grassland matrix, a mix of small wetlands and shrublands, and readily use various agricultural lands (Merrill et al. 1999).

Regional geographic scale. Regional-scale species exist at the broadest geographic scale; they include wide-ranging animals, such as migrating ungulates and top-level predators. These species use resources over millions of hectares or more, including natural to semi-natural matrix and embedded large- and small-patch ecosystems. Examples include caribou (*Rangifer tarandus*) of northern North America, mountain lions (*Puma concolor*) in the West, jaguar (*Panthera onca*) in Latin America, American bison (*Bison bison*) of the Great Plains, migratory fishes in big rivers, and many species of migratory birds.

The exact geographic scale of a particular ecosystem or species in a given area or region will depend on several factors, including the environmental setting and the species' life-history characteristics. Some regions, such as the North American Great Plains and the southeastern Coastal Plain, are characterized by flat topography and large-scale disturbance regimes (e.g., landscape fires, hurricanes). Natural matrix ecosystems in these areas (e.g., tallgrass prairie, longleaf pine forests) originally occurred over millions of hectares. In contrast, steep topography and more localized disturbance regimes (e.g., ridgetop fires, landslides, ice storms) in the southern Blue Ridge Mountains have produced a patchwork vegetation pattern. Matrix ecosystems in this latter region may be an order of magnitude smaller than in the Great Plains or Coastal Plain. Moreover, an animal species may use resources at different scales in different regions (e.g., mountain lions may be regional-scale species in one region and coarse-scale species in another). Consequently, it may be difficult to assign an ecosystem or species to an exact scale, particularly because basic, region-specific life-history information is lacking for most species. Thus, we define the extent of the four geographic scales generally and with overlapping values to account for these regional differences.

Functional conservation areas—sites, landscapes, and networks

Conservation of biodiversity at multiple levels of biological organization and spatial scales is complex and requires two key steps: explicit identification and protection of the focal ecosystems and species in a given area, and adequate identification and protection of the associated multiscale ecological processes that support and sustain those ecosystems and species (Pickett et al. 1992, Meyer 1997). These requirements are met within what we call functional conservation areas. We define a functional conservation area as a geographic domain that maintains focal ecosystems, species, and supporting ecological processes within their natural ranges of variability.

Functional conservation areas have several characteristics. First, the size, configuration, and other design characteristics will be determined by the focal ecosystems, species, and supporting ecological processes. Second, a conservation area is functional if it maintains the focal biotic and abiotic patterns and processes within their natural ranges of variability over time frames relevant to conservation planning and management (e.g., 100–500 years). Third, functional conservation areas do not necessarily preclude human activities, although their functionality or integrity may be greatly influenced by such activities (Redford and Richter 1999). Finally, functional conservation areas at all scales may require ecological management or restoration to maintain their functionality (e.g., prescribed burning, invasive species removal).

We define three types of functional conservation areas: sites, landscapes, and networks (Figure 2). The defining characteristics of these conservation areas are the ecosystems and species they are designed to conserve. Functional sites aim to conserve a small number of ecosystems and/or species within their natural ranges of variability at one or two scales below regional; functional landscapes seek to conserve many ecosystems and species within their natural ranges of variability at all scales below regional (i.e., coarse, intermediate, and local); and functional networks are integrated sets of sites and landscapes designed to conserve regional-scale species within their natural ranges of variability.

Examples of functional sites are areas intended to conserve one or more rare or endangered species or uncommon ecosystems, often at the local scale. Such areas constitute the majority of nature preserves in the United States. These areas are functional sites if they adequately conserve (or restore through management) the focal biodiversity and their sustaining ecological processes (e.g., fire, flood, dispersal, pollination) within their natural ranges of variability (Poiani et al. 1998). Although ecosystems and species of concern at functional sites are not necessarily easy to conserve, they are relatively few and easy to identify, and they share similar sustaining ecological processes (e.g., an assemblage of fire-dependent prairie plants and butterflies, or a wetland complex and its associated rare species). In some cases, and especially over the long term, functional sites for even small-patch ecosystems and local-scale species may require large areas to be conserved.

In functional landscapes, ecosystems and species of conservation concern are more numerous than at functional sites. Functional landscapes typically encompass the full terrestrial to aquatic (and sometimes marine) gradient, and they require a diversity of sustaining ecological processes. Functional landscapes usually exist within a human- or multiple-use context and commonly span diverse land ownership.

It is the degree to which an area comprehensively conserves biodiversity at three or more scales, rather than its size, that distinguishes a functional landscape from a functional site. Indeed, the size of a conservation area alone does not ensure the protection of biodiversity at all scales (Simberloff 1998). For example, conservation areas in the southeastern Coastal Plain that seek to conserve coarse-scale red-cockaded woodpeckers (*Picoides borealis*) must encompass extensive expanses of longleaf pine matrix with significant old growth and sparse understory (Hardesty et al. 1997). Woodpecker conservation therefore requires protection and fire management of large areas. Yet

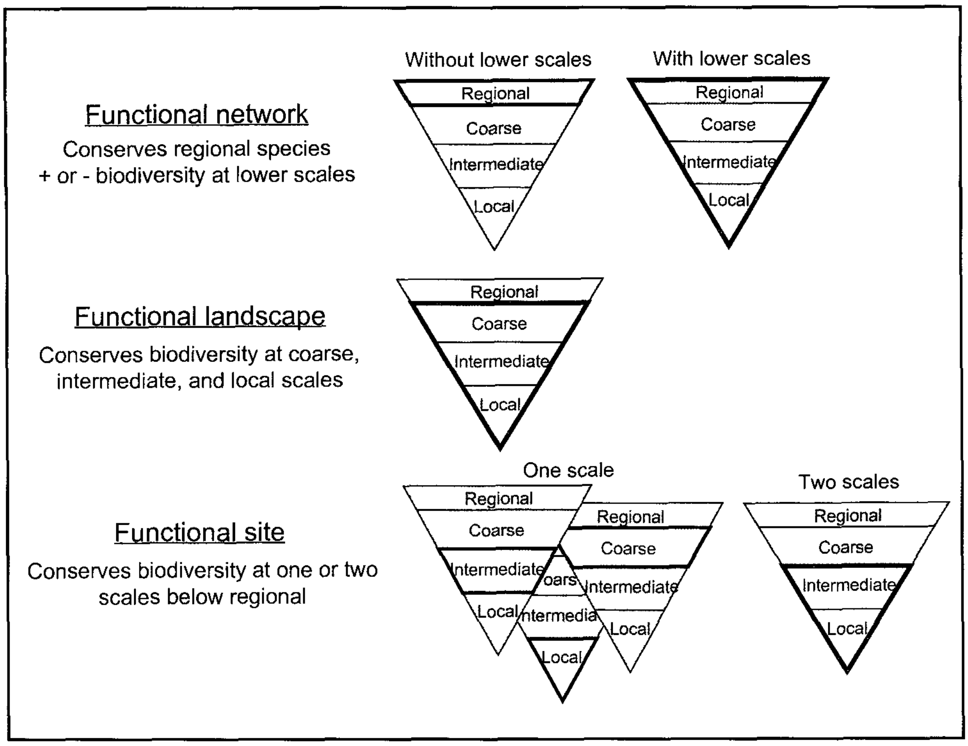


Figure 2. Definitions of functional sites, landscapes, and networks and their relationships to biodiversity at various spatial scales.

it is possible to conserve woodpeckers and their required habitat and still degrade nonfocal biodiversity (e.g., streams and wetlands and their associated species). Similarly, a functional site focused on intermediate-scale aquatic species might require attention to large watershed areas because of the need to maintain natural hydrologic and water chemistry regimes. Again, full protection of the habitat and ecological processes that sustain aquatic species may not be enough to conserve terrestrial biodiversity, such as upland rare plants, matrix forest, or forest interior birds.

Finally, functional networks provide adequate spatial context, configuration, and connectivity to conserve regional-scale species with or without explicit consideration of biodiversity at finer scales. Sites or landscapes within functional networks can be arranged contiguously within one region or in several adjacent regions to protect species such as migrating ungulates or grizzly bears (*Ursus arctos horribilis*). Conversely, sites or landscapes may form a series of stepping stones spread over many regions to protect migratory species, such as certain birds, insects, and bats.

Although functional networks are intended to conserve regional-scale species, some functional networks may also include explicit attention to biodiversity at other scales. Functional networks with a multiscale perspective differ fundamentally from networks focused solely on regional-scale species. Examples of networks focused on regional-scale species alone have been articulated for several areas of the United States (e.g., Noss 1993, Cox et al. 1994); such designs do not explicitly consider the area or actions necessary to conserve finer-scale ecosystems and species within these regions. Functional networks that continue to conserve both regional-scale species and biodiversity at all finer scales include the Brooks Range of Alaska, the northern Rocky Mountains in the United States and Canada, and the Serengeti–Mara system in Tanzania and Kenya.

Conservation at multiple scales

Implementing a functional conservation approach requires practitioners to first identify the ecosystems or species toward which conservation efforts are or will be directed. Conservation organizations and natural resource agencies should strive for a comprehensive, multiscale approach, in which they direct conservation efforts toward biodiversity at the coarsest scale an area can support and then determine the extent to which ecosystems and species at finer scales can be targeted. Thus, new conservation areas should, wherever possible, be functional landscapes or contribute to a functional network. If an area cannot support a functional landscape or regional-scale species, a functional site should be delineated and conserved at the highest possible scale.

Determining the appropriate focus for a conservation area is an iterative process, in which initial assumptions about site or landscape functionality are examined more rigorously over time. Periodic refinement of the initial focus is warranted following management, research, or other ongoing observations. For example, areas designed to conserve one or a few local- to intermediate-scale ecosystems or species may be logically extended to include coarser patterns (e.g., a site focused on a large-patch riparian mosaic may be expanded to conserve adjacent high-quality upland matrix), whereas an area that is designed with a coarse-scale focus may, in light of new findings, need to be refocused downward to include finer-scale patterns (e.g., a site focused on red-cockaded woodpeckers may need to be expanded to conserve high-quality small-patch wetlands and their associated local-scale species).

Directing conservation efforts toward biodiversity at coarse scales while integrating ecosystems and species at finer scales has many benefits. Attention to coarse-scale ecosystems—particularly outright conservation of matrix types—has generally been neglected by private conservation efforts. Matrix ecosystems are relatively common and typically do not contain many rare species (Franklin 1993). However, an intact matrix is often key to the long-term persistence of large- and small-patch ecosystems and lower-scale species.

Multiscale conservation can also offer a more comprehensive and conservative strategy for protecting little-known species and genetic diversity, especially if conservation areas encompass broad physical and biological gradients and capture unique environmental features (Hunter et al. 1988). Such comprehensive gradients offer greater protection against and capacity to accommodate human-induced environmental change (e.g., climate change, acid deposition, invasive species; Hunter et al. 1988). However, understanding and monitoring complex multiscale conservation areas will often require substantial resources.

Functional networks should also, to the extent that it is scientifically sound, seek to conserve ecosystems and species at finer scales. Conserving species at a single scale (even an umbrella species at the coarse or regional scale) can miss important linkages, ecological processes, and biodiversity at other scales (Simberloff 1998).

Ecological attributes for evaluating functionality

Identifying and protecting functional conservation areas is challenging, given the complexity of both ecological and human issues at any given place (Stanford and Poole 1996). One of the most important but difficult tasks in the process is to determine a conservation area's degree of functionality or ecological integrity. Such information is critical in formulating appropriate conservation, management, and restoration strategies and in evaluating current and potential human uses. Assessment of ecological integrity or functionality is a relatively undeveloped area in applied ecology. Although almost all natural systems and species are influenced by a multitude of past and current human activities (Breitburg et al. 1998), the effects of these activities on biodiversity are often complex and sometimes obscure. Thus, assessing an area's functionality should be an iterative process based on accumulated knowledge.

The list of potential attributes that can be examined to assess a conservation area's functionality or integrity is exceedingly long (e.g., Noss 1990). Applied conservation organizations rarely have the ability and resources to examine all of them. Based on our experiences at many conservation sites and landscapes, we suggest evaluating four well-known attributes (which encompass the critical patterns and processes at most conservation areas). Ideally, other area-specific attributes could be added as time and resources allow (e.g., Hardesty et al. 1997). The four attributes are composition and structure of the focal ecosystems and species; dominant environmental regimes, including natural disturbance; minimum dynamic area; and connectivity.

Evaluating these attributes at functional sites and even functional networks should be relatively straightforward. However, evaluating the attributes for functional landscapes is more challenging. To assess functional landscapes, a subset of ecosystems and species must be selected that adequately identifies the patterns and processes needed to conserve the entire functional landscape (i.e., for planning) and that provides information on landscape functionality over time (i.e., for adaptive management and monitoring). Focal ecosystems and species selected for these two purposes may not necessarily be the same. In both cases, however, it is important to choose ecosystems and species at all focal spatial scales (e.g., Hansen and Urban 1992, Block et al. 1995, Hardesty et al. 1997, Breininger et al. 1998). Exemplary focal ecosystems and species for functional landscape planning and monitoring include those that require specific management or conservation strategies, those that integrate or span various parts of the terrestrial–aquatic gradient (e.g., species that use wetlands and uplands), those that are known to be sensitive to alterations in the key attributes (i.e., indicator species), those that play a primary role in sustaining key ecological processes (i.e., keystone species), and those that are readily monitored. For nongovernmental conservation organizations, a focus on endangered species will also provide a good link to the mission of state and federal agency partners. Several guidelines provide further insights for defining and selecting indicator, focal, and keystone species (e.g., Noss 1990, Cairns et al. 1993, Noss and Cooperrider 1994, Power et al. 1996, Noon et al. 1997, Simberloff 1998).

Composition and structure. For purposes of biodiversity conservation, functionality or integrity of a conservation area can perhaps best be judged by the extent to which the composition and structure of the focal ecosystems and species are within their natural ranges of variability. Even for conservation areas with intact or nearly intact ecological processes, conservationists should not assume that focal ecosystems and species are compositionally and structurally intact. For example, invasive nonnative species can displace natives, completely altering ecosystem composition, while general ecological processes such as fire and flood are still maintained. In addition, preliminary evidence shows that compositional and structural integrity may be critical in maintaining internal stability, productivity, and resilience of the ecosystem itself (e.g., Johnson et al. 1996, Naeem 1998).

Key compositional and structural components for species are age structure, evidence of reproduction, population size or abundance, and, when possible, genetic diversity and minimum viable populations. Key compositional and structural components for ecosystems are more complex and can include abundance of invasive species (non-native or native), presence of keystone species, presence of species that indicate unaltered ecological processes, abundance of important prey species, existence of characteristic species diversity, evidence of reproduction of dominant species, and evidence of vertical strata or layering. Composition and structure of focal large-patch and matrix ecosystems can also include the spatial distribution and juxtaposition of internal patch types or seral stages, the presence of characteristic patch types, and the extent of fragmentation and non-natural or semi-natural land uses.

Dominant environmental regimes. To determine the functional status of a conservation area, practitioners must understand and evaluate dominant and sustaining environmental regimes relative to the ecosystems and species of concern. Environmental regimes can be diverse and can vary considerably among conservation areas. Important dominant environmental regimes include grazing or herbivory, hydrologic and water chemistry regimes (surface and groundwater), geomorphic processes, climatic regimes (temperature and precipitation), fire regimes, and many kinds of natural disturbance.

Natural disturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). Natural disturbance is a key aspect of environmental regimes and plays a critical role in the dynamic fluctuation of habitat availability and biotic diversity. When environmental regimes and natural disturbances are pushed outside their natural ranges of variability by human influences, changes in ecosystems and species will follow.

There are few places where completely unaltered environmental regimes and natural disturbances currently exist, particularly those operating at broad scales. For example, Alaska and northern Canada may be the only remaining areas in North America that have truly natural fire regimes. Even Yellowstone National Park, where most lightning fires are allowed to burn, does not have a completely natural fire regime (Romme and Despain 1989). Thus, it is critical to evaluate the potential to restore regimes and disturbances through active management (e.g., prescribed fire, prescribed floods, managed grazing).

Minimum dynamic area. Another consideration in assessing functionality of sites, landscapes, and networks is their necessary size or extent. Dynamic natural disturbances may greatly influence local populations and ecosystems, even causing their local extirpation. Within large-patch and matrix ecosystems, disturbances create a diverse, shifting mosaic of successional stages and physical settings of different origin and size (Bormann and Likens 1979). Although many small-patch ecosystems tend to be more stable in their location, disturbances also influence their composition and structure, and populations of species within them can fluctuate widely. Thus, metapopulation spatial structure and processes may be essential to sustain local-scale species and small-patch ecosystems, for which replication and connectedness would be more important than size (Fahrig and Merriam 1985).

Regardless of whether a shifting mosaic or metapopulation model is most appropriate, the rate of recovery of an ecosystem or species at any scale following disturbance is influenced strongly by the availability of nearby organisms or propagules and biological "legacies" (e.g., seed banks, underground biomass) for recolonization (Holling 1973). When recolonization sources are available and plentiful, recovery will be optimal. The area needed to ensure survival or recolonization has been called the minimum dynamic area (Pickett and Thompson 1978). For certain small-patch ecosystems and species, this concept may be better described as "minimum dynamic number."

Minimum dynamic area has already become an important consideration in the design of conservation areas and should be a primary factor in assessing functional sites, landscapes, and networks. For example, Shugart and West (1981) suggested that, as a rule of thumb for forested ecosystems, the minimum dynamic area is typically 50 times the mean disturbance patch size. Baker (1992) emphasized that reserves should be large relative to maximum disturbance sizes, thus minimizing their vulnerability to catastrophic loss of organisms, reducing the chance of disturbance spreading to adjacent developed lands, and minimizing the influences of adjacent lands on the size and spread of disturbance at the margins. In addition, Peters et al. (1997) suggested that a minimum dynamic area must be large where disturbance events are either large or common. They recommended that managers use simulation models to analyze system response to natural disturbances and to determine the minimal area needed to absorb the largest disturbance event expected within a 500–1000-year period. Developing scientific estimates of minimum dynamic area and metapopulation structure for biodiversity at different scales, or guidelines as to how to develop such estimates efficiently, is one of the critical frontiers of applied conservation biology.

As well as considering natural disturbance regimes, it may also be critical to estimate the minimum conservation area needed to actively manage for broad-scale disturbances, in cases where disturbance regimes will never be fully intact. For example, many sites need to be large enough to burn or graze on a rotational basis and to satisfy a variety of species and habitat requirements (Biondini et al. 1999).

Connectivity. Connectivity includes several key concepts: focal species have access to all habitat and resources needed for life cycle completion, focal ecosystems and species have the ability to recover following disturbance, and focal ecosystems and species have the ability to respond to environmental change (Saunders et al. 1991, Stanford and Ward 1992, Rosenberg et al. 1997). For example, access to backwater areas on a floodplain during

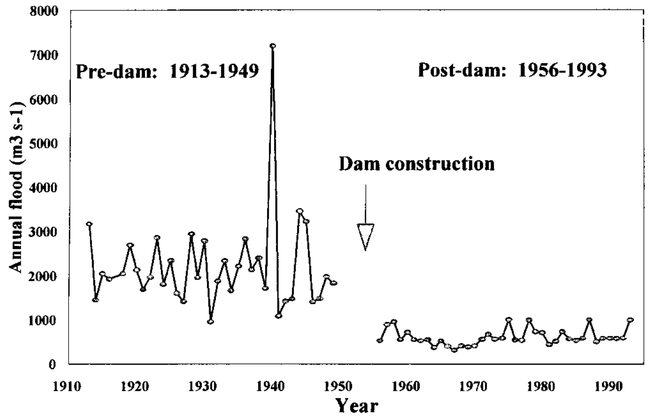


Figure 3. Hydrograph of annual flood levels (m^3/s) for the Roanoke River, North Carolina, shows changes in natural flow regime. Large dams began operating on the Roanoke River in 1956.

annual spring floods may be critical for fish spawning (Sedell et al. 1990). Enabling local- to regional-scale migrations of various ecosystems and species will become critical with global warming. Functional conservation areas must allow for such movements by encompassing entire elevational gradients or spanning many geological substrates, depending on the needs of the focal systems and species (Hunter et al. 1988). For example, to fully conserve vernal pools over a 100-year time frame, it may be necessary to protect pools that vary in size, depth, hydroperiod, and substrate, such that component species have the natural abiotic template on which to evolve over time.

The degree to which a site, landscape, or network is connected and the ability of organisms to move, disperse, migrate, or recolonize varies with the species (e.g., Hansen and Urban 1992, Pearson et al. 1996). A landscape that is fragmented to a black bear, for example, may be continuous to a local-scale insect (Wiens and Milne 1989). Thus, connectivity must be considered in light of the wide range of life-history characteristics and ecological processes of the focal biodiversity. This situation reiterates the importance of selecting focal biodiversity at multiple scales for complex functional landscapes.

A word on natural ranges of variability. Ecological patterns and processes as described above are highly dynamic in time and space (Morgan et al. 1994). To protect focal biodiversity over long time frames, practitioners need to understand, describe, and, where possible, quantify and conserve the range of these natural biotic and abiotic fluctuations (Noss 1985, Swanson et al. 1993, Poff et al. 1997, Richter et al. 1997). For example, flood disturbances have been suppressed in the majority of rivers in the Northern Hemisphere (e.g., Figure 3). When a key disturbance regime such as flooding is pushed outside (typically below) its natural range of variation, ecosystems and species that depend on conditions associated with large floods may not be viable over the long term (Poff et al. 1997).

Unfortunately, present understanding of most biotic and abiotic variation and its causes is rudimentary. Biological monitoring data are limited and often inadequate for describing long-term variation. Data sets from long-term research sites (Bildstein and Brisbin 1990) and breeding bird surveys are several significant exceptions. Furthermore, for most locations in the United States, historical records exist that at least allow researchers to reconstruct or characterize environmental regimes, such as stream flow, temperature, and precipitation.

In addition, a variety of methods have proven useful for reconstructing presettlement or historic patterns and processes to help define natural ranges of variability (Noss 1985, Morgan et al. 1994, Birks 1996, Delcourt and Delcourt 1996, Poiani et al. 1996, Foster et al. 1998). These methods include simulation modeling, historical accounts and early land surveys, interpretation of historic aerial photographs, and paleoecological evaluations of sediments, charcoal, tree rings, pollen, and seed banks. Thermographs, rainfall hyetographs, hydrographs (e.g., Figure 3), or output from simulation models can be summarized statistically (e.g., magnitude, intensity, duration, timing, frequency, spatial extent, and rate of change) to describe and quantify natural ranges of variability (Baker 1992, Morgan et al. 1994, Richter et al. 1996). Also, when data are not available for a particular ecosystem or species, deductions about cause-and-effect relationships can sometimes be drawn from reference areas or similar ecosystems and organisms (Arcese and Sinclair 1997).

Ecological models (particularly simulation models) can aid in assessing acceptable variability in focal patterns and processes (e.g., Lauenroth et al. 1998, Maddox et al. 1999). When human land and water use regularly push key environmental parameters outside their natural ranges, or threaten to do so in the future, a predictive model can provide a potent tool for understanding possible consequences for focal biodiversity. Simple rule-based state-and-transition models are particularly useful for understanding vegetation dynamics (e.g., Poiani and Johnson 1993, Johnson 1994, Ellison and Bedford 1995, Richter 1999). Population dynamics models can also predict the cumulative effect of repeated perturbation on focal species (Ruggiero et al. 1994, Noon et al. 1997).

The challenges of implementation

The overall framework outlined in this article may be most useful if employed several times during the course of ongoing conservation activities. As a first step, ecological attributes can be rapidly evaluated to identify focal ecosystems and species for a new or existing conservation area. As a second step, ecological attributes must be evaluated in greater depth and detail during ongoing planning and adaptive management to examine and refine the initial assumptions. Evaluating the attributes using data, simulation models, historical analyses, or monitoring and research projects may be appropriate during this second stage.

Evaluation of both ecological patterns and processes, however, represents a major challenge for conservation scientists and practitioners. Among the greatest problems is translating the four functional attributes into effective, useful, and measurable specifics for planning, monitoring, and assessment. For example, are there rules of thumb for determining minimum dynamic area for various ecosystem types? Do thresholds exist for environmental regimes (e.g., flooding), fragmentation, or invasive species beyond which ecological integrity is diminished to unacceptable limits? In addition, identifying a subset of focal ecosystems or species (i.e., indicators, keystones, or guilds) that may be used to gauge broader site or landscape functionality is proving difficult (Landres et al. 1988). Even focusing on keystone species appears to miss many vital components of an ecosystem (Franklin 1993), although further research may reveal more promising results (Simberloff 1998).

In the human arena, implementing conservation across multiple scales requires unprecedented levels of coordination among federal, state, and local institutions, both public and private. Many small-patch ecosystems and local-scale species can still be approached in a site-based fashion using the traditional strategies of land purchasing or easements. However, effective conservation at a local scale is generally management intensive and may be the most expensive option in the long run. Conserving functional landscapes, by contrast, typically requires greater initial investments and extensive partnership networks, including a diverse cast of stakeholders. At the scale of the functional network, evaluation of existing managed areas, regionwide threats, public input, zoning, and education become essential tools, again requiring extensive coordination and cooperation among landowners.

A TNC case study illustrates the application of the framework described in this article. Drawing from our 14 years of experience along the Yampa River in northwestern Colorado, we describe the challenges and benefits derived from a multiscale, functional conservation approach.

The Yampa River case study

The Yampa River originates along the continental divide of the Rocky Mountains in northwestern Colorado at an elevation of approximately 3400 meters above sea level and flows 300 km to join the Green River near the Utah border. The upper tributaries in the watershed are small, steep-gradient montane streams that are generally 1–4 m wide. These tributaries coalesce to form the 30–40 m wide mainstem of the river, which runs through broad, gently sloping valleys and, occasionally, narrow canyons. As the river flows west, it crosses from the Colorado Rocky Mountains, which are dominated by coniferous forests, aspen stands, and montane shrublands, to the Wyoming Basin region, which is dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*). Along the longitudinal gradient of the river and its tributaries, the riparian vegetation varies greatly. Average annual precipitation in the headwaters exceeds 150 cm per year, most of which falls as snow, resulting in a snowmelt-driven flood regime. Flows in the mainstem peak in late May to early June, ranging from an average low of 14–28 m^3/s to an average high of 140–280 m^3/s.

Conservation focus. TNC's work along the Yampa River over the past 14 years illustrates the evolution from conservation focused on rare biodiversity to the design and management of a functional conservation area. Between 1986 and 1996, TNC acquired several hundred acres along the Yampa River, primarily to conserve mature stands of the globally rare box elder–narrowleaf cottonwood/red-osier dogwood (*Acer negundo–Populus angustifolia/Cornus sericea*) riparian forest. In the mid-1990s, TNC developed a conceptual ecological model that would provide a broad framework for understanding the dynamics of the riparian system along the mainstem of the Yampa River. The model quickly revealed that the globally rare forest TNC initially sought to protect was in fact only one of several shifting patch types within a larger dynamic riparian ecosystem (Figure 4). That is, the rare forest type was not a stable, small-patch ecosystem that could be managed out of context from the overall large-patch riparian mosaic. Thus, TNC's conservation focus evolved from protecting a single riparian patch type at a local scale to protecting the entire large-patch riparian mosaic at an intermediate scale.

A second expansion in scale? More recent discussions of Yampa River conservation center around whether focus should shift again, from a functional site aimed at the large-patch riparian mosaic and associated fine- and intermediate-scale species to a functional landscape that seeks to conserve biodiversity at all scales. Matrix ecosystems surrounding the Yampa River at both high and low elevations remain relatively unaltered. For example, the USDA Forest Service manages the majority of the upper watershed as part of the Routt National Forest. A greater percentage of private ownership exists lower in the basin, but much of the Wyoming big sagebrush matrix in this area remains relatively intact. In addition, several important coarse-scale species appear to be supported by the sagebrush matrix and other embedded patch ecosystems within the watershed, including elk (*Cervus elaphus*) and Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*). The latter species is declining over much of its range due to the loss, degradation, and fragmentation of sagebrush habitat throughout the West. However, the northwestern Colorado population of sharp-tailed grouse is the largest within the state and apparently stable, and it may represent an important conservation opportunity (Giesen and Braun 1993).

The Yampa River watershed may also provide one of the

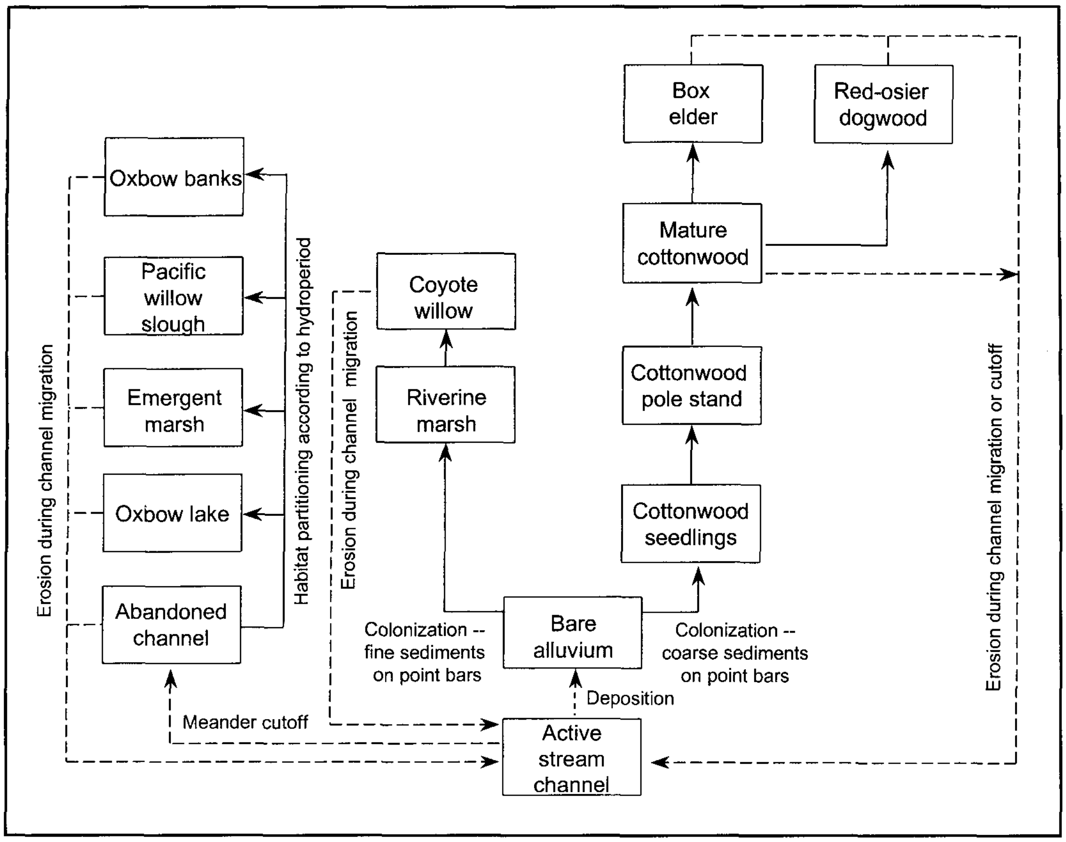


Figure 4. Conceptual ecological model of riparian patch dynamics along the Yampa River, Colorado. Boxes indicate the various patch types within the riparian mosaic, solid arrows indicate biotic succession, and dashed arrows represent geomorphic changes. Figure reprinted from Richter (1999).

necessary functional landscapes for regional-scale species in the area. Bald eagles (*Haliaeetus leucocephalus*) nest along the Yampa River during the summer, several hundred greater sandhill cranes (*Grus canadensis tabida*) use the valley as a critical staging area during their spring and fall migrations, and many neotropical migratory birds nest and forage within the riparian corridor. Adequate protection of such regional-scale species obviously requires more than just the Yampa River watershed. However, TNC biologists may need to explicitly consider these regional-scale species in their conservation and management efforts. Further information is needed before the conservation effort at Yampa River can undergo a second expansion in scope, but such issues illustrate the multiscale, iterative process we advocate in this article.

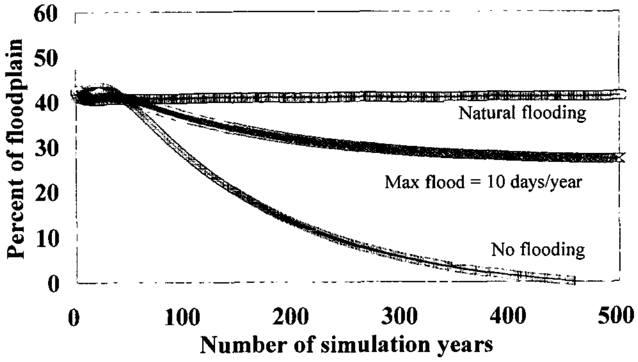
Composition and structure. Clearing for agriculture, lumber, and firewood has directly altered riparian vegetation along the Yampa River since European settlement in the 1870s. Although much of the clearing occurred before 1938, when the first aerial photographs were taken, total cover of mature cottonwood forest along the Yampa River near Hayden, Colorado, declined by 18% between 1938 and 1989. Even more striking, the average size of mature stands declined by 62% during that period (Noble 1993).

In addition to these broad-scale changes, the remaining forest stands have changed in composition and structure. Historic aerial photographs indicate that in heavily used areas, the crowns of individual trees were more widely spaced than in more inaccessible areas (such as islands). Thinning presumably increased light availability and the abundance of shade-intolerant grasses for livestock forage while decreasing native shade-tolerant understory species. Today, many previously thinned stands have responded by asexual root sprouting and filling in gaps with young cottonwood trees (Richter 1999), resulting in mixed-aged stands. A more typical age structure of cottonwood forests consists of even-aged cohorts of trees that result from stand establishment during episodic flood events. Forest thinning and subsequent asexual reproduction may have also resulted in decreased genetic diversity within stands (Richter 1999). Evaluating such changes in the composition and structure of the Yampa River's riparian mosaic has helped elucidate appropriate restoration strategies capable of reversing these trends.

Dominant environmental regimes. To increase understanding of the dynamic fluvial processes that shape and sustain the focal biodiversity along the Yampa River, TNC developed a conceptual ecological model of the riparian ecosystem (Figure 4; Richter 1999). Construction of the model helped to define the complex relationships between hydrologic and geomorphic processes and the internal patch types that make up the riparian mosaic, thus highlighting the key environmental regimes that must be conserved.

A quantitative computer simulation model was subsequently developed to determine the extent to which past or future human influences alter these relationships. The model was developed for a 19 km reach of the riparian corridor upstream from Hayden. Data sources for model construction and calibration included geographic infor-

Figure 5. Simulation of Yampa River riparian dynamics. Variability in the abundance of mature cottonwood patches within the riparian ecosystem (from Figure 4) is predicted by a simulation model over a 500-year period associated with natural and altered flooding regimes (Richter and Richter in press). The graph illustrates the predicted abundance of mature cottonwood with natural flooding regime, with cumulative annual flooding duration limited to a maximum of 10 days each year (i.e., flood control), and with no flooding. Restricting flood duration to a maximum of 10 days each year shortened floods in 22% of the simulation years. Floods were defined as the flow equal to or greater than 125% of bankfull discharge.



mation system (GIS) maps of the riparian ecosystem derived from aerial photography, analysis of existing long-term streamflow records, calculation of geomorphic process rates (e.g., lateral channel migration), sampling of vegetation composition and structure, and tree dating (Richter 1999).

State variables used in the simulation model were the internal patch types that make up the Yampa River's riparian mosaic as defined by the conceptual model in Figure 4. The model simulated changes in the area and proportion of each patch type (i.e., percentage of the riparian area occupied) over time. Initial values for the area occupied by each patch type were derived from a 1938 vegetation map. Fluxes among state variables (represented by the arrows in Figure 4) were computed in the model by sets of difference equations that were updated during annual time steps. These equations represented the rates at which internal patch creation and destruction were expected, based on various levels of flooding and rates of plant succession. Patch-type abundance predicted at the end of the simulation period (1938–1989) was compared to actual patch-type abundance in 1989 as determined from aerial photos.

Discrepancies between model results and actual data initiated several new observations and insights. Channel sinuosity and lateral channel migration rates had changed relatively abruptly over the simulation period, suggesting channel instability. The Yampa River may have crossed a geomorphic threshold from a meandering to a braided channel. Narrowleaf cottonwood requires fresh alluvial deposits for seedling establishment, where subsequent floods will not destroy newly germinated seedlings. Although sufficient fresh depositional surfaces were still being produced in recent decades, these deposits no longer formed within protected meander bends but instead formed as mid-channel islands and lateral bars. Such changes in geomorphic processes have direct implications for cottonwood establishment, and they likely result in part from decreased bank stability due to deforestation of stream banks during the past century (Richter 1999).

After recalibration and validation of current and historic conditions, the model was used to explore the potential impacts of future hydrologic alterations due to a growing human population in the Yampa River watershed (Richter and Richter in press). Statistical evaluation of many flood variables (e.g., magnitude of flood peak, duration of bankfull flow) during model development suggested that the duration of floods may be the most important variable driving riparian dynamics. If the annual number of days in which streamflow exceeded 125% of the bankfull discharge were limited to 14 days or less, then the mean abundance of some patch types, such as mature cottonwood, would deviate outside the 90% confidence limits of natural flow regime simulations (Figure 5; Richter and Richter in press). Thus, the natural variability in flood duration will need to be conserved in the future to maintain the current level of functionality at this site.

Minimum dynamic area. The minimum dynamic area for the Yampa River riparian ecosystem must maintain recolonization sources for each internal patch type and provide room for the geomorphic processes that reshape the floodplain and create and destroy the complete array of patch types. Human alteration of riparian vegetation, along with an associated reduction in the width of the riparian corridor, may have important ramifications for minimum dynamic area. Remaining stands of riparian vegetation are primarily located adjacent to the active stream channel. Preferential clearing of vegetation has eliminated stands on the outer edges of the floodplain that would be most secure from catastrophic floods. Not only is riparian vegetation more vulnerable to widespread destruction by floods, but future sources of propagules for post-disturbance recovery may also be severely reduced as a result of a narrowed and fragmented riparian corridor.

Extensive human alteration of riparian vegetation has made it difficult to determine the natural extent (particularly the width) of the riparian corridor before European settlement. However, geologic maps depict the extent of alluvial deposits, which can be used to approximate the river's active "meander belt" since the Pleistocene. These alluvial deposits are equivalent to the maximum potential extent of the riparian ecosystem over the long term. Even the largest contemporary flood is unlikely to eliminate vegetation across the entire width of the meander belt, allowing some refugia and sources of propagules for recolonization.

However, the exact extent of the minimum dynamic area for this riparian ecosystem remains undefined, and it likely differs from the maximum potential floodplain. Further analysis is warranted to more precisely define minimum dynamic area. In the interim, restoration of previously cleared areas located at the outer fringes of the floodplain and revegetation of denuded stream banks should be considered a high priority because they would help restore geomorphic processes. Until a catastrophic flood occurs, the long-term implications of an altered floodplain may not be realized.

Connectivity. A great deal of ecosystem and species diversity along the Yampa River is attributable to the steep elevation gradients in the watershed. The ability of the riparian ecosystem and associated species within the watershed to shift their elevation range as global climate change occurs may be critical to their long-term persistence. Therefore, representation of the entire elevation gradient along the Yampa River, from high-elevation headwater tributaries to lower-elevation reaches within the Wyoming Basin region, will likely be important for conservation of focal biodiversity.

Longitudinal connectivity between protected riparian areas within the watershed will also be important to maintain flows of energy, matter, and species. For example, propagules of riparian species commonly originate upstream or upwind of the open sand bars where they germinate. Lateral connectivity—particularly the interface of the riparian mosaic with uplands—is also important, especially if the conservation focus expands to include coarse- or regional-scale biodiversity. Currently, the longitudinal connectivity of this system has not been significantly altered within the watershed, but clearing of riparian forest has compromised lateral connectivity.

Conclusions

The Yampa River case study illustrates the importance and challenge of clearly defining the focus and scale of biodiversity conservation at a given site. Evaluating the four functional attributes relative to the target riparian ecosystem also provided important insights into management and restoration strategies needed to conserve the site.

Applying the core concepts articulated in this article to other conservation sites is essential because effective biodiversity conservation depends on functionality. Existing conservation areas, as well as remaining undeveloped or moderately altered areas, should be evaluated for their optimum potential to conserve biodiversity at multiple scales. In particular, it is critically important to identify and prioritize all remaining functional landscapes for future conservation. Such areas will likely remain viable over long time frames and provide the diverse environmental gradients and regimes necessary for biodiversity to respond to global change.

Yet, even with the integrated, multiscale framework presented in this article, great challenges exist for conservation practitioners. The natural ranges of variability for most patterns and processes will remain imperfectly known, with the possible exception of dominant processes that have been monitored for long periods (e.g., flooding regimes). Moreover, practitioners must somehow decide, based on extremely limited knowledge, the extent and level to which human impacts can be tolerated. A high priority for research is therefore to identify levels or thresholds of human alteration to natural ranges of variability that lead to unacceptable impoverishment of biodiversity.

The ability to incorporate the criteria we have outlined in applied conservation decisions is rapidly increasing as new tools and techniques (e.g., GIS, remote sensing imagery, simulation modeling, and long-term data sets) become available. New ecological research, increasing availability of powerful new technologies for assessing ecological systems, and growing conservation focus on the dynamic nature of ecological systems will all help practitioners incorporate ecosystem- and landscape-level concepts into biodiversity conservation to the greatest extent possible.

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