US Environmental Protection Agency
Office of Federal Activities

CONSIDERING ECOLOGICAL PROCESSES IN ENVIRONMENTAL IMPACT ASSESSMENTS

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INTRODUCTION

The purpose of this guidance is to provide information to U.S. Environmental Protection Agency (EPA) offices on how to incorporate ecological considerations into the preparation and review of environmental impact assessments. Environmental impact assessment as used in this document means any assessment of the consequences of human activities on the environment. Examples include documents done under the National Environmental Policy Act, risk analyses, and assessments prepared to support decision-making by EPA or other organizations. The report builds on previous Office of Federal Activities (OFA) reports entitled, *Consideration of Terrestrial Environments in the Review of Environmental Impact Statements, Habitat Evaluation: Guidance for the Review of Environmental Impact Assessment Documents, Evaluating Mining Impacts, Evaluating Grazing Impacts, and Evaluation of Ecological Impacts from Highway Development.* It is consistent with the approach to environmental impact assessment described in the Council on Environmental Quality (CEQ) report, *Incorporating Biodiversity Considerations Into Environmental Impact Analysis Under the National Environmental Policy Act*. It is anticipated that in addition to being used by EPA, this document will also be used by other government and private organizations as they consider the effects of human activity on the environment.

The analysis of ecological impacts has traditionally focused on single species and familiar habitats. The current challenge for environmental impact assessment is to broaden analyses to capture all aspects of biological diversity, especially the interactions within and among ecosystems. Conservation biology is the discipline that attempts to prescribe methods for maintaining and restoring biodiversity. This relatively new field embraces four fundamental objectives supporting the overarching goal of maintaining the native biodiversity of a region in perpetuity (Noss and Cooperrider 1994):

- Represent, in a system of protected areas, all native ecosystem types and seral stages (of community succession) across their natural range of variation.
- Maintain viable populations of all native species in natural patterns of abundance and distribution.
- Maintain ecological and evolutionary processes, such as natural disturbance regimes, hydrological processes, nutrient cycles, and biotic interactions.
- Manage landscapes and communities to be responsive to short-term and long-term environmental change and to maintain the evolutionary potential of the biota.

The third objective, "maintain ecological and evolutionary processes," is the focus of this document. Noss and Cooperrider (1994) state that "considering process is fundamental to biodiversity conservation because process determines pattern." Specifically, ecological processes such as natural disturbance, hydrology, nutrient cycling, biotic interactions, population dynamics, and evolution determine the species composition, habitat structure, and ecological health of every site and landscape. Only through the conservation of ecological processes will it be possible to (1) represent all native ecosystems within the landscape and (2) maintain complete, unfragmented environmental gradients among ecosystems.

Protecting ecosystems is increasingly being recognized as essential to protecting public health and the environment. Many government efforts realize now that clean air and clean water depend not only on the control of hazardous discharges, but on the maintenance of ecosystem services that assimilate wastes. For example, a recent report by the Commission on a Sustainable South Florida recommends redirecting growth away from the Everglades and other ecologically valuable places because tourism, drinking water, and the fishing industry depend on a healthy natural environment (Noss and Peters 1995). The Interagency Ecosystem Management Task Force (1995) report, *The Ecosystem Approach: Healthy Ecosystems and Sustainable Economies*, describes the federal investment in and commitment to ecosystem analysis. Many individual agencies have been developing an ecosystem approach to management, and some have incorporated their initiatives into their NEPA analyses.

Implementing such ecosystem approaches requires a clear understanding of the term "ecosystem." An ecosystem is the interconnected assemblage of all species populations that occupy a given area and the physical environment with which they interact. Ecosystems provide not only valuable products and essential services, but also opportunities for recreation and aesthetic enjoyment. Examples of ecosystem services include purifying air and water, providing flood control, building fertile soils, and producing food, fiber, and other natural resources for human consumption. Healthy forests, for example, provide wood products, sequester man-made gases that cause global warming, and control erosion that degrades water quality and fisheries, and support wildlife and rare species.

Maintaining healthy ecosystems requires protecting their integrity. Ecological integrity is the long-term health and sustainability of the interactions among the physical, chemical, and biological elements of an ecosystem. Integrity is diminished when the quality of habitat is degraded, the distribution and abundance of species is altered, or natural ecological processes are degraded. Threats to ecological integrity, and ecosystems in general, include habitat destruction, overharvesting of resources, invasion of exotic species, fire suppression, environmental pollution, and global climate change, among others. The most severe habitat destruction occurs when a natural ecosystem is converted to an artificial system (as when a forest is replaced by a shopping center), but habitats can be destroyed or degraded through intensive agriculture and grazing, clearcut logging, mining, roadbuilding, housing and other development, and damming and channelization of streams (Noss et al. 1995).

That ecosystems in all 50 states face significant threats to their integrity is well documented in a recent National Biological Service report (Noss et al. 1995) and additional analysis by Noss and Peters (1995). These reports demonstrate that some ecosystems have virtually disappeared (primarily grasslands, savannas, and barrens) since European settlement and that many have lost more than half of their original area. Ecosystem types that have declined by more than 85% include old-growth forests in all states except Alaska, limestone cedar glades in the South and Midwest, wetlands of most types in the Midwest, Gulf Coast pitcher plant bogs, coastal redwood forests and vernal pools in California, dry forests in Hawaii, and native beach communities and sea grass meadows in many coastal areas. Although information on aquatic ecosystems is more scarce, 81% of fish communities nationwide are known to have been adversely affected by human activities (Judy et al. 1984).

What is less well known is how the ecological processes inherent to these ecosystems have been altered, degraded, or completely lost. Leslie et al. (1996) state that "...communities are organized and patterned; they typically have a structure that is to some degree predictable from the regional pool of species available, the local climatic and soil conditions, historical events in the area, and the presence of dominant species." Therefore, it is incumbent on analysts to consider all three components of ecosystems: composition (what is out there), structure (how is it distributed in time and space), and function (what it does). More than simply measuring more things, an adequate environmental impact analysis requires developing an understanding of ecological processes and how they contribute to sustaining ecological integrity and the elements (species, habitats, and services) society is concerned with.

As a practical matter, the analyst conducting an environmental impact assessment needs to focus on individual ecological processes and how they can be affected by human activities through cause and effect. At the same time, the analyst needs to maintain an "ecological mindset" that focuses on the interconnectedness of processes within ecosystems. Pickett et al. (1997) has posited a framework for the "flux of nature" that describes ecosystems as open systems that (1) can be externally regulated, (2) may have multiple dynamic pathways, (3) do not necessarily have a single stable equilibrium state, (4) include natural disturbance as a natural part of the system, and (5) incorporate humans as components.

The following pictorial, "A Cascade of Ecosystem Effects Through 10 Major Ecological Processes," illustrates the interconnectedness within ecosystems using a hypothetical construction project and following the chain of indirect effects arising from the altered hydrologic pattern caused by creating impervious surfaces. This example points out that doing only one thing is impossible in ecology--there are always indirect effects and they usually manifest themselves through ecological processes.

CONSIDERING THE CONSEQUENCES OF ALTERING ECOLOGICAL PROCESSES

While the consequences on ecosystems will vary with the project and the environmental setting, it is useful for analysts to begin their evaluation by investigating discrete ecological processes. As shown in the pictorial, there are ten ecological processes that effectively capture ecosystem functioning and should be evaluated for adverse effects:

1. Habitats Critical to Ecological Processes

2. Pattern and Connectivity of Habitat Patches

3. Natural Disturbance Regime

4. Structural Complexity

5 Hydrologic Patterns

6. Nutrient Cycling

7. Purification Services

8. Biotic Interactions

9. Population Dynamics

10. Genetic Diversity

The remainder of this document contains a section on each ecological process that begins with a concise definition of the process and is followed by a more detailed discussion of what constitutes the process and how it should be described in NEPA analyses. The section then describes how the ecological process is affected by human activities that may be the focus of NEPA analyses. Lastly, the section discusses ways of mitigating adverse effects on the ecological process. Throughout the sections, examples are used to help the reader identify the processes that may be affected by his project and better understand which ecosystems the processes are likely to occur in. To emphasize the integrated nature of ecological processes, the links among processes are also highlighted in these sections.

REFERENCES

Council on Environmental Quality (CEQ). 1993. *Incorporating Biodiversity Considerations Into Environmental Impact Analysis Under the National Environmental Policy Act*. CEQ, Executive Office of the President, Washington, DC.

Judy, R.D., P.N. Seeley, T.M. Murray, S.C. Svirsky, M.R. Whitworth, and L.S. Ischinger. 1984. 1982 National Fisheries Survey, Volume I. Technical Report: Initial Findings. U.S. Environmental Protection Agency and U.S. Fish and Wildlife Services, Washington, DC. FWS/OBS-84/06.

The Interagency Ecosystem Management Task Force report. 1995. *The Ecosystem Approach: Healthy Ecosystems and Sustainable Economies. Volumes 1-3.* Washington, DC. June 1995, November 1995, October 1996.

Leslie, M. G.K. Meffe, J.L. Hardesty, and D.L. Adams. 1996. *Conserving Biodiversity on Military Lands: A Handbook for Natural Resource Managers*. The Nature Conservancy, Arlington, VA.

Noss, Reed F., and Allen Y. Cooperrider. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press.

Noss, R.F., E.T. LaRoe III, and M.J. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biological Report 28. National Biological Service, U.S. Department of Interior, Washington, DC. 58 pp.

Noss, R.F. and R.L. Peters. 1995. Endangered Ecosystems: A Status Report on America's Vanishing Habitat and Wildlife. Defenders of Wildlife, Washington, DC.

Pickett, S.T.A., R.S. Ostfeld, M. Shachak, and G.E. Likens. 1996. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity*. Chapman and Hall, New York.

1. HABITATS CRITICAL TO ECOLOGICAL PROCESSES

DEFINITION

At the level of a landscape or region, certain natural habitat types are especially important for the ecological functioning or species diversity of the ecosystem. Unusual climatic or edaphic (soil-based) conditions may create local biodiversity hotspots or disproportionally support ecological processes such as hydrologic patterns, nutrient cycling, and structural complexity. For these reasons, preservation of specific habitats (usually the remaining natural areas within the landscape) should be a priority.

WHAT CONSTITUTES HABITATS CRITICAL TO ECOLOGICAL PROCESSES AND HOW DO THEY CONTRIBUTE TO ECOLOGICAL INTEGRITY?

Historically, environmental impact assessments have identified the potential impacts of project activities on habitats of concern. Initially such habitats were confined to those supporting commercially or recreationally important fish and game species. With the passage of the Endangered Species Act and Section 404 of the Clean Water Act, both critical habitat for threatened and endangered species and wetlands received close attention. In recent years, an appreciation for the vast array of other species and habitats (e.g., old growth forests) that are potentially affected by human activities has arisen under the banner of biodiversity conservation. Conservation biologists have been virtually unanimous in their contention that it is the destruction of habitats worldwide that most threatens biodiversity and the sustainability of ecosystems.

Within the landscape, certain habitats disproportionately contribute to ecosystem functioning. In general these are the remaining natural areas, especially those that integrate the flows of water, nutrients, energy, and biota through the watershed or region (Polunin and Worthington 1990). The concept is analogous to that of keystone species that have a disproportionate effect on community structure (Paine 1969). Forests, rangelands, and aquatic ecosystems all have unique or critical habitats that support the provision of ecosystem services within the landscape. In addition, ecotones (the boundary or transition zone between plant communities) may be especially important for processing resources, as they frequently have more individuals and species (Hunter 1990).

The best understood examples of habitats critical to ecosystem functioning are wetlands. Wetlands provide flood storage, water purification, and nursery habitat for fish, birds, and other animals. A saltmarsh can be thought of as a "keystone ecosystem," because it provides critical nutrients and organic matter to the adjacent estuary (Hunter 1996). Calls for no net loss of wetlands recognize the need to maintain a critical amount of wetlands to sustain regional ecosystem services. Another example of a keystone ecosystem would be a river that mediates the spread of fire and sustains fire-sensitive islands. Forests are well known as critical habitats for many species, providing food, shelter, and climate amelioration. Remnant forest patches as also important as a refuge during migration and as a source for recolonization of other patches. Less appreciated is the fact that natural forests can absorb twice as much water as plantation forests, slowing runoff and erosion (Noss and Peters 1995).

HOW SHOULD HABITATS CRITICAL TO ECOLOGICAL PROCESSES BE DESCRIBED?

Recognizing that certain habitats, or types of habitats, are of special value for ecosystem functioning, and responding to the conclusion of the EPA Science Advisory Board that habitat alteration and destruction are among the greatest risks to ecological and human welfare, the OFA prepared its guidance, *Habitat Evaluation: Guidance for the Review of Environmental Impact Assessment Documents* (U.S. EPA 1993). This guidance document discussed, in general terms, habitat conservation and assessment methods and identified lists of habitats of concern in six major habitat regions of the conterminous United States plus Alaska and Hawaii. Approximately a dozen "principal habitats of concern" per region (e.g., longleaf pine-wiregrass and New Jersey pine barrens) were identified within each general habitat category (e.g., old-growth pine forest of the Southeastern Forests and Croplands region). The document discussed in some detail the primary impacts on each habitat of concern from the most relevant of eight major human activities (see below).

Since the OFA habitat guidance document was prepared, concern for identifying critical or endangered ecosystems across the country has intensified. The Nature Conservancy and the affiliated state natural heritage programs are continuing their impressive work of identifying the rarest vegetative communities in each state and have recently developed a national classification system for existing, natural terrestrial vegetation. The system is hierarchical with five upper levels based on physical structure of the vegetation and two lower levels based on floristics. Currently over 4,300 vegetation types have been identified at the finest level of the classification hierarchy, the association (most occurring in the continental United States, Hawaii, and a small part of Alaska). The Federal Geographic Data Committee has accepted the framework as an information and classification standard to be used by all federal agencies (FGDC 1997). Grossman et al. 1994 reported that The Nature Conservancy and the Natural Heritage Network describe 371 globally rare terrestrial and wetland plant communities in the United States (another 482 globally rare communities are known but not adequately inventoried or mapped).

On the national scale, the most important compilation of critical or sensitive habitats is the former National Biological Service report (Noss et al. 1995), *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation*. This and the related report by Noss and Peters (1995) provide a status report on the condition of habitats most critical for maintaining biodiversity and sustaining ecosystem functioning across the country. The benefit of these reports it that they identify and list (unfortunately the majority of habitats are not yet mapped) ecosystem types that ultimately can be measured and mapped as species have been and thus managed for their conservation. The ecosystem types include many plant communities or associations, but also habitats based on soil type (e.g., sandstone barrens), physical structure (e.g., caves), age (e.g., old-growth ponderosa pine), and condition (e.g., ungrazed semiarid grasslands or free-flowing streams).

The National Biological Service study found that some ecosystems have virtually disappeared (primarily grasslands, savannas, and barrens) since European settlement and that many have lost more than half of their original area. Ecosystem types that have declined by more than 85% include old-growth forests in all states except Alaska, limestone cedar glades in the South and Midwest, wetlands of most types in the Midwest, Gulf Coast pitcher plant bogs, coastal redwood forests and vernal pools in California, dry forests in Hawaii, and native beach communities and sea grass meadows in many coastal areas (Noss and Peters 1995). Although information on aquatic ecosystems is more scarce, 81% of fish communities nationwide are known to have been adversely affected by human activities (Judy et al. 1984). Noss and Peters (1995) conclude that the 21 most endangered ecosystems in the United States are the following:

- South Florida landscape
- Southern Appalachian spruce-fir forest
- Longleaf pine forest and savanna
- Eastern grasslands, savannas, and barrens
- Northwestern grasslands and savannas
- California native grasslands
- Coastal communities in the lower 48 states and Hawaii
- Southwestern riparian forests
- Southern California coastal sage scrub
- Hawaiian dry forest
- Large streams and rivers in the lower 48 states and Hawaii
- Cave and karst systems
- Tallgrass prairie
- California riparian forests and wetlands
- Florida scrub
- Ancient eastern deciduous forest
- Ancient forest of the Pacific Northwest
- Ancient red and white pine forest, Great Lakes states
- Ancient Ponderosa pine forest
- Midwestern wetlands
- Southern forested wetlands

In addition to paying special attention to human activities in these imperiled large-scale ecosystems (and those listed in the OFA habitat guidance), analysts should consult the state natural heritage program for finer-scale vegetation types that are of special concern. In the future, the national vegetation classification with be further developed through a cooperative effort among the Ecological Society of America, The Nature Conservancy, and federal agencies (Loucks 1996).

HOW ARE HABITATS CRITICAL TO ECOLOGICAL PROCESSES AFFECTED BY HUMAN ACTIVITIES?

The proximate cause of ecosystem or habitat loss is land conversion or other activities that degrade natural habitats to the point that they become different environments. Ecosystems are also degraded when habitats remain but their composition, structure, or function is substantially altered. The ultimate cause of habitat loss and degradation is the expanding human population and the need to secure land and water for human uses. The following major activities may cause the loss of habitats critical to ecological processes:

• Land conversion to industrial and residential land use

• Land conversion to agriculture

• Land conversion to transportation

• Timber harvesting practices

• Grazing practices

• Mining practices

• Water management practices

• Military, recreational, and other activities

Environmental analyses of these activities arise during both broad programmatic reviews and specific project environmental impact statements. The following common projects entail significant impacts to habitats and may require federal review:

• Community and public land use development, including planning, regulation, and federal funding for building construction and highway development

• Renewable resource use and development (logging and grazing) on public lands or requiring permits

• Energy production, including petroleum, natural gas, and coal development, extraction, generation, transmission, and use

- Non-energy mineral resource development, processing, management, transport, and use

- Water projects and permits for wetland modification

- Natural resources conservation, including protection of environmentally critical areas

The loss and degradation of forest habitat is common to many projects. While forests, in general, have been recognized as habitat for wildlife species, the values associated with different forest types has only more recently been considered. Specific forest communities, particularly old-growth stands, support sensitive species and ecological processes that cannot be sustained in other forest types. In the most celebrated example, the conflict between timber production and endangered species survival in the Pacific Northwest was addressed in the "Draft Supplemental Environmental Impact Statement on Management of Habitat for Late-Successional and Old-Growth Forest Related Species Within the Range of the Northern Spotted Owl" (U.S. Forest Service and Bureau of Land Management 1993). This study focused scientific scrutiny on the sensitive old-growth forest habitat that is critical to sustaining the ecological integrity by evaluating effects on a wide range of species (including invertebrates) and ecological processes in key watersheds (affecting salmon runs). Logging activities in old-growth forests all over the country face the same dilemma.

The loss of wetland habitats is another widespread issue. Wetlands contain a disproportionately large number of threatened and endangered species for their limited area (Noss and Peters 1995), many confined to specific types of wetlands (i.e., those with unusual plant communities). Although wetlands constitute only about 5% of the land base in the conterminous United States, nearly 30% of listed animals and 15% of listed plants are associated with wetlands. The case is even more acute for riparian areas in the southwestern United States where 80% of the wildlife habitat and 70% of rare and endangered vertebrates occur on only 2% to 4% of the land (Johnson 1989). Wetlands often occur because of a unique combination of topography, soil types, and hydrology. For this reason, the loss of specific wetlands can dramatically alter regional fauna and flora. Caves and desert springs that support endemic (geographically restricted) amphibian, fish, and invertebrate fauna may be the most extreme examples of sensitive wetland habitat critical to maintaining local biodiversity.

HOW CAN ADVERSE EFFECTS ON HABITATS CRITICAL TO ECOLOGICAL PROCESSES BE MITIGATED?

Mitigating the loss of habitats critical to ecological processes requires a rigorous search for their presence, a thorough review of the threats they face, and careful consideration of ways to avoid impacts to them in the design and implementation of projects. Often, effectively mitigating the loss of habitat can only be achieved by avoiding conversion of the habitat to another land use. Rarely is restoration or compensation an adequate mitigation for the loss of these habitats.

Therefore, mitigation is typically a siting issue, where construction and degrading activities are located a distance from the habitats of concern. Where habitat degradation is the issue, such as results from logging and grazing, careful management measures can be implemented to ensure protection of the habitats of concern. In such cases, the basic principal is to manage for uncommon habitats (Noss and Cooperrider 1994). Streams, seeps, and swamps make a disproportionate contribution to biodiversity and should be spared from intensive uses. For example, in designing a logging or grazing plan, it is important to leave remnant forest buffers around any rare, sensitive, and highly dispersed habitats.

The following specific mitigation measures are taken from the OFA habitat guidance document (U.S. EPA 1993). The measures are grouped by category of human activities likely to affect habitats critical to ecological processes:

• <u>Land conversion to industrial and residential land use</u>. Effective mitigation of land conversion activities can sometimes be obtained only by avoiding impacts on rare or unusual habitat types. Successful siting can preserve habitats of concern if all possible impact scenarios are accounted for. Barring avoidance of sensitive habitats, protective land management practices, restoration, or compensation must be implemented.

• <u>Land conversion to agriculture</u>. Conversion to agricultural land is a special concern in rangelands with increasing irrigation potential. Land conversion to agriculture can cause groundwater overdraft, salinization of topsoil and water, reduction of surface water, high soil erosion, and destruction of native vegetation. Mitigations include more conservative irrigation techniques and improved drainage systems. Soil conservation techniques vary from windbreaks to contour plowing, stripcropping, rotation of crops, conversion to grass, and/or minimum tillage. In the case of unique riparian or wetland habitats, hydrological and contamination concerns are especially important. Construction or resource management activities require the use of sediment filter strips and other means of intercepting offsite contaminants. Road building and structural "improvements" must not result in altered hydrological regimes. Desert habitats are especially vulnerable to mechanical disruption by vehicles and machinery. Where rare plant types exist or where habitats are unstable (e.g., sand dunes), recreational access may have to be limited.

• <u>Land conversion to transportation.</u> Amelioration of impacts from land conversion to transportation uses requires special mitigation measures. As with all land conversion, the construction of highways and power-line corridors is primarily a siting issue. Avoidance of sensitive habitats may be accomplished by modifications to the route design, and the extent of disturbance can be limited by careful construction practices. However, fragmentation of the larger area is unavoidable in the case of land conversion to transportation corridors. Many structural mitigation strategies can be used to lessen the impact on animal movement across transportation routes. Primarily, these include the construction of fences and underpasses. The goal of these structural measures should be to mimic the natural movement and migration patterns of the affected species.

• Timber harvesting practices. At a minimum, the production of wood products from an area must not exceed the sustainable level if the ecological integrity of a forested area is to be maintained. Where sensitive forest types exist, logging may be completely prohibited or constrained to specific methods to prevent habitat loss or degradation. In other areas, more extreme harvesting methods may be allowed or prescribed to establish or maintain desired forest conditions. Acceptable methods will vary according to local forest ecology and the desired future condition of the site. Analysis of harvesting techniques must be based upon an analysis of the structure and diversity of the forest canopy, midstory, and understory. The harvesting technique employed must be based upon sound logging and timber management prescriptions and demonstrate its capability to maintain vertical diversity (foliage height diversity), horizontal diversity (interspersion, edge, juxtaposition, patchiness), and a mixture of live and dead wood. Specific timber harvesting operations should be designed to preserve the structure and diversity of the natural forest habitat. Clear cutting is acceptable only when it is possible to replicate natural ecological processes.

• Grazing practices. Traditional management for production of livestock based on forage production relative to a mythical average has effectively converted natural grasslands to degraded rangelands dominated by exotic species. Recently, some range managers have begun to base range condition on deviation from an ideal range or ecological climax. The problem for habitat conservation is that the proportion of rangeland climax habitats has greatly decreased, similar to the case with old-growth forest. Although there remain disagreements over proper management methods, more effective use of ecological analyses of range condition will likely improve the management of rangelands. Successful riparian management requires unique solutions to the specific condition at each site, but should include the following general principles: (1) include riparian areas in separate pastures with separate objectives and strategies, (2) fence or herd stock out of riparian areas to let vegetation recover, (3) control the timing of grazing to keep the stock off streambanks they are most vulnerable to erosion and to coincide with the physiological needs of plants, (4) provide more rest to the grazing cycle to increase plant vigor or encourage more desirable species, and (5) limit grazing intensity.

• Mining practices. Mitigation of mining impacts involves siting issues, technological solutions to eliminate contamination, and restoration programs. The major mitigations for oil and gas extraction and production are the proper siting of rigs, reserve pits, processing facilities, and roads where they will have minimal impacts on habitats of concern. Most important for coal and mineral mining is the siting of mining operations and tailing ponds to avoid habitats of concern, wetlands, riparian areas, and recharge areas. Specific mitigation measures depend on the type of mining and the specific process causing impacts. It is generally best to minimize the area affected as it is unlikely that even the disrupted soils and sediments can be restored. In addition to minimizing the area disturbed, activities should be timed to avoid disturbing nearby plants and animals during crucial periods of their life cycle.

• Water management practices. The regulation and damming of streams can eliminate habitat (especially riparian vegetation) through flooding or the draining of land. Dams and water diversion significantly change downstream flow regimes, levels of winter floodwater, dry-season flow rates, and riparian-zone soil moisture. Downstream areas lose pulse-stimulated responses while upstream areas are affected by water impoundment and salt accumulation. Mitigation involves measures to mimic natural flow regimes and habitat creation to compensate for lost habitat types. Restoration and mitigation banking are often pursued as mitigation measures for direct wetlands alterations.

• Military, recreational, and other activities. An awareness of the ecological consequences of specific activities is essential to effective mitigation. The Army's Integrated Training Area Management (ITAM) program is a comprehensive means of matching military training mission objectives with effective natural resource management. If such a plan is instituted, it is likely that careful coordination of the siting and timing of training operations will dramatically reduce habitat impacts. General mitigation principles should address the (1) timing and siting of operations, (2) calculation of allowable use for tracked vehicles, and (3) fire suppression during artillery practice.

Links between critical habitats and other ecological processes. The presence of specific habitats is closely linked to the other ecological processes discussed in this document. By definition, the abundance and distribution of critical habitats affects the pattern and connectivity (Ecological Process [EP]-2). Natural disturbance regimes (EP-3) and hydrologic patterns (EP-5) effectively maintain these habitats and their structural complexity (EP-4). Critical habitats such as wetlands are well known for their nutrient cycling (EP-6) and purification services (EP-7). Habitats obviously support the species with characteristic genetic diversity (EP-10), population dynamics (EP-9), and biotic interactions (EP-8).

REFERENCES

Federal Geographic Data Committee (FGDC). 1997 Vegetation classification standard, FGDC-STD-005. http://www.fgdc.gov/standards/documents/standards/vegetation

Grossman, D.H., K.L. Goodin, and C.L. Reuss. 1994. Rare Plant Communities of the Conterminous United States: An Initial Survey. The Nature Conservancy, Arlington, VA.

Hunter, M.L., Jr. 1990. *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice Hall, NJ.

Hunter, M.L., Jr. 1996. *Fundamentals of Conservation Biology*. Blackwell Science, Cambridge, MA.

Johnson, A.S. 1989. The thin green line: Riparian corridors and endangered species in Arizona and New Mexico. In Preserving Communities and Corridors. Defenders of Wildlife, Washington, DC. pp. 35-46.

Judy, R.D., P.N. Seeley, T.M. Murray, S.C. Svirsky, M.R. Whitworth, and L.S. Ischinger. 1984. 1982 National Fisheries Survey, Volume I. Technical Report: Initial Findings. U.S. Environmental Protection Agency and U.S. Fish and Wildlife Services, Washington, DC. FWS/OBS-84/06.

Loucks, O. 1996. 100 years after Cowles: a national classification for

vegetation. Bulletin of the Ecological Society of America 77:75-76.

Noss, Reed F., and Allen Y. Cooperrider. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press.

Noss, R.F., E.T. LaRoe III, and M.J. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biological Report 28. National Biological Service, U.S. Department of Interior, Washington, DC. 58 pp.

Noss, R.F. and R.L. Peters. 1995. Endangered Ecosystems: A Status Report on America's Vanishing Habitat and Wildlife. Defenders of Wildlife, Washington, DC.

Paine, R.T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91-93.

Polunin, N. and E.B. Worthington. 1990. On the use and misuse of the term 'ecosystem.' *Environmental Conservation* 17:274.

U.S. Environmental Protection Agency. 1993. Habitat Evaluation: Guidance for the Review of Environmental Impact Assessment Documents. U.S. EPA, Office of Federal Activities. January.

U.S. Forest Service and Bureau of Land Management. 1993. Draft Supplemental Environmental Impact Statement on Management of Habitat for Late-Successional and Old-Growth Forest Related Species Within the Range of the Northern Spotted Owl. Portland, OR. July.

2. PATTERN AND CONNECTIVITY OF HABITAT PATCHES

DEFINITION

At the landscape level, natural ecosystems have a characteristic pattern and connectivity of habitat patches. The amount and juxtaposition of these patches supports the movement of species and the transfer of materials (energy and nutrients) among habitats. Prior to human settlement, natural landscapes were characterized by large expanses of contiguous habitat. The fragmentation of these areas into disconnected and isolated patches can significantly disrupt ecological integrity.

WHAT CONSTITUTES THE PATTERN AND CONNECTIVITY OF HABITAT PATCHES AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

Forest, rangeland, and aquatic ecosystems all have characteristic patterns of habitat patches; in addition, the larger landscape can be viewed as a mosaic of adjacent ecosystems. To understand a landscape's patterns (such as the mosaic of agricultural lands and forest), its elements (such as landscape corridors), and its processes (such as habitat fragmentation) requires a holistic approach (Barrett and Bohlen 1991). It is important to note that all naturally regenerating forests are "patchy," i.e., the trees and associated organisms do not occur in uniform patterns (Harris and Silva-Lopez 1992). This ecological patchiness, however, generally involves natural gradations among forest types and is very different than the fragmentation that occurs when a formerly contiguous forest is converted into a matrix of forested and nonforested habitat.

Ecological and evolutionary processes produce the pattern and connectivity of landscapes. For example, Levin (1976, 1978) showed that biotic predator-prey interactions, combined with spatial movement, can result in patchy spatial patterns of populations. Paine and Levin (1981) demonstrated that natural regimes of disturbance and recovery also produce spatial pattern. In turn, landscape patterns influence the ways organisms move on the landscape (Wiens and Milne 1989) and the ways they utilize resources (O'Neill et al. 1988b). Dispersal processes and spatial pattern interact to separate competitors and make coexistence possible (Comins and Noble 1985).

Landscape connectivity involves the linkages of habitats, species, communities, and ecological processes at multiple spatial and temporal scales (Noss 1991). In a natural landscape, connectivity among like habitats is usually high. Topography and microclimate difference may create barriers to species dispersal, especially between waterbodies. In isolated habitats, populations are more susceptible to environmental catastrophes and invasion by exotic species (Harris 1984, Soule 1987).

The size of habitat patches has important implications for ecological integrity. Small habitat patches (e.g., habitat islands) have fewer species than large patches and more isolated habitat patches have fewer species than less isolated patches (Hunter 1996). Large patches have more species because (1) a large patch will always have a greater variety of environments that provide niches for species that would be absent otherwise, (2) a large patch is likely to have both common and uncommon species while a small patch is likely to have only common species (not only are area-sensitive species excluded, but the sampling effect itself will result in fewer species in small patches), and (3) a small patch will have, on average, smaller populations that are more susceptible to becoming extinct. Even though the applicability of island biogeography theory (MacArthur and Wilson 1967) is more limited for habitat patches than for true islands, the concept of increased extinction rates in smaller areas is important. Habitat patches that are isolated from similar habitat patches by great distances or inhospitable terrain are likely to have fewer species than less isolated patches because (1) relatively few individuals of a given species will immigrate into an isolated patch and (2) fewer mobile species will visit isolated patches because it is inefficient to do so (Hunter 1996).

HOW SHOULD THE PATTERN AND CONNECTIVITY OF HABITAT PATCHES BE DESCRIBED?

Landscape ecology is an emerging discipline that considers the spatial and temporal patterns and exchanges across the landscape, the influences of spatial heterogeneity on ecological processes, and the management of spatial heterogeneity for society's benefit (Risser et al. 1984). Using GIS technologies, landscape ecologists have developed a useful suite of indicators of landscape pattern from remote sensing information. The primary categories of indicators describe the arrangement of habitat patches as dominance (few or many habitat types), contagion (like types clumped or not clumped), and fractal dimension (simple or complex patterns) (O'Neill et al. 1988a, 1994).

Of greatest interest to the analyst is the measurement of habitat fragmentation. The following parameters can be used to determine habitat patch size, edges, heterogeneity and dynamics, context, and connectivity within the landscape (Harris and Silva-Lopez 1992):

- the amount, composition, and distribution of residual habitat
- the abruptness of gradation between remaining patches
- the continuity or disruption of the distribution and movement of native organisms
- the composition and structure of the vegetation that now constitutes the landscape matrix
- the compositional pattern of the overall landscape

Also of interest are the types of landscape corridors. Corridors can be classified into five basic types: disturbance corridors, planted corridors, regenerated corridors, environmental resource corridors, and remnant corridors (Barrett and Bohlen 1991). The type of corridor has implications for environmental impact assessment and mitigation design.

HOW IS THE PATTERN AND CONNECTIVITY OF HABITAT PATCHES AFFECTED BY HUMAN ACTIVITIES?

The fragmentation of habitat has been implicated in the decline of biological diversity and the ability of ecosystems to recover from disturbances (Flather et al. 1992). Habitat fragmentation is the process by which a natural landscape is broken up into small patches of natural ecosystems, isolated from one another in a matrix of lands dominated by human activities (Hunter 1996). The principal cause of worldwide habitat fragmentation is the expanding human population converting natural ecosystems into human-dominated ecosystems, primarily agriculture. Obvious examples of anthropogenic effects on landscape patterns and connectivity include clearcutting for lumber, urbanization, construction of transportation corridors, the draining of wetlands, and the conversion of forest and prairies into crop and grazing systems.

Human activities can either reduce or increase connectivity. Humans have created artificial barriers to species dispersal, while at other times eliminating natural barriers. In the former situation, isolated populations become more vulnerable to extinction owing to reduced access to resources, genetic deterioration, increased susceptibility to environmental catastrophes and demographic accidents, and other problems (Harris 1984, Soule 1987). In the latter situation, it becomes easier for exotic organisms to invade native communities, resulting in the homogenization of floras and faunas.

Richard Forman has developed a terminology for describing the fragmentation process (cited in Hunter 1996) as follows:

- **dissection** of a natural landscape begins with the building of a road or other linear feature;
- **perforation** of the landscape occurs when some of the natural habitats are converted into agricultural or other modified land uses;
- **fragmentation** occurs when more and more of the landscape is converted so that the modified lands coalesce and the natural habitat patches are isolated from one another; and
- **attrition** occurs when more of the natural patches are converted, becoming smaller and farther apart

The permanent conversion of natural ecosystems to human land uses is an obvious case of fragmentation. In other cases, such as clearcutting areas that naturally regenerate, whether the activity constitutes fragmentation depends on whether the clearcut is extensive enough to constitute a significant barrier to the movement of plants and animals (Spies et al. 1994). In general, the greater the difference between the natural ecosystem and the human-dominated ecosystem, the more likely it is that the fragmentation will isolate the biota in the natural fragment. The degree of isolation depends on the species, its dispersal abilities, and its ability to survive in the modified environment.

Although habitat loss itself is important, the consequences of fragmentation are greater than expected based solely on the area of habitat destroyed. The most obvious example is area-sensitive species that cannot maintain populations in limited areas of even otherwise high quality habitat. Raptors, large cats, and grizzly bears are prominent examples of species that need extensive home ranges and thus avoid smaller habitat fragments. Road construction and second home development are fragmenting the remaining large expanses of wildlands needed for such large carnivores. Species with small home ranges, such as songbirds, may also avoid small fragments if they prefer the interior of large habitat patches (Robbins et al. 1989) or select patches large enough to support other members of their species (Stamps 1991).

As discussed above, population size is reduced in small habitat fragments. For example, the suburban sprawl that is reducing the coastal sage habitat area in southern California, may affect the viability of populations of gnatcatchers and other species (Reid and Murphy 1995). In addition, the migration of animals that travel between habitats seasonally (e.g., birds and fish) or during their life cycle (e.g., amphibians) can be impeded by fragmentation. The segmentation of large rivers into series of reservoirs has had dramatic effects on the migration of anadromous salmonids across the country. Highway construction that dissects forest habitat affects the migration of several frog and salamander species to their spring breeding ponds, often resulting in major road kills. Over longer periods, climate change may require species to shift their entire geographic ranges, an impossibility when fragmentation has eliminated intervening suitable habitat (Peters and Lovejoy 1992)

Another important consequence of fragmentation is the increase in perimeter area or "edge" habitat (Hunter 1996). Simple geometry dictates that small fragments have more edge in relation to their area than large fragments and that the less like a circle the fragment is the greater is its perimeter. The consequences of increased edge include (1) the change in physical conditions (organisms near the edge are subjected to more wind, less moisture, and greater temperature extremes) and (2) invasion by species from the surrounding disturbed habitat (e.g., competitors such as weeds and predators such as rats, cats, and people). Perhaps the best studied effects are the high levels of nest predation and brood parasitism on forest birds nesting near forest-farmland edges (Wilcove et al. 1986, Paton 1994). Population declines in forest-interior birds, including many migratory songbirds, has been ascribed to these effects of fragmentation as well as to losses of wintering habitat in Latin America.

The fragmentation of habitat not only changes the biotic interactions that structure ecosystems, but can also adversely affect nutrient cycling. In terrestrial ecosystems, the most vulnerable abiotic factor is soil fertility, a condition that can be degraded by leaching of nutrients when vegetation-free patches are created (Ewel 1986). The loss of soil fertility can affect plant competition and influence the forage quality of plant parts. The leaching of nutrients also creates a burden for aquatic systems in the form of undesirable nutrient enrichment. Especially in warm, humid climates, the presence of actively growing vegetation can mean the difference between net retention and loss of nutrients; a process that is affected by the size and duration of vegetation-free patches. In general, there is a critical size of vegetation-free patch, probably a size that is unique to each combination of soil, vegetation, and climate, below which nutrient losses are likely to negligible.

HOW CAN ADVERSE EFFECTS ON THE PATTERN AND CONNECTIVITY OF HABITAT PATCHES BE MITIGATED?

Landscape ecology principles can be used to adjust the design and implementation of a project to minimize the isolation and edge effects on species and ecological processes. These principles are now finding an audience among landscape architects and land-use planners (Dramstad et al. 1996), and deserve expanded attention from environmental impact analysts.

Management of land development and mitigation of adverse impacts on the pattern and connectivity of habitats should follow these conservation principles (Reid and Murphy 1995):

- species that are well distributed across their native ranges are less susceptible to extinction than a species confined to small portion of their ranges
- large blocks of habitat containing large populations of target species are superior to small blocks of habitat containing small populations
- blocks of habitat that are close together are better than blocks that are far apart
- habitat that occurs in blocks that are less fragmented internally is preferable to habitat that is internally fragmented
- interconnected blocks of habitat are better than isolated blocks, and habitat corridors or linkages function best when the habitat within them resembles habitat that is preferred by the target species
- blocks of habitat that are roadless or otherwise inaccessible to people better conserve target species then do roaded and easily accessible habitat blocks

Noss (1990) has provided the following more specific recommendations for managing habitat pattern and connectivity in forestry activities:

- <u>Manage on spatial scales appropriate to all objectives</u>. Patch shapes on managed lands are quite regular, even if their edges are rounded. Managed land produces a mosaic of homogeneous patches very unlike the mosaic of uneven-sized and uneven-shaped, heterogeneous patches produced by natural disturbances. For these reasons, land management should mimic natural patch shapes and mosaics. In general, forest vegetation treatments should vary more in size and shape than under the current system, and they should be aggregated to increase effective patch size and minimize fragmentation (this will also reduce the cost of building roads).

- Manage for linear features as well as for patches. Forest riparian corridors can serve as snow-free highways for terrestrial animals moving up and down hills; therefore, the widths currently based on shade buffers should be widened to lessen snow depths in these corridors. Even strips of wind-firm trees that cannot provide forest-interior microclimates should be included to offer cover, perches, and food for dispersing species. If it is impossible to provide continuous corridors, linear archipelagoes of remnant patches may have value for more mobile species.

Links between the pattern of habitats patches and other ecological processes. The pattern and connectivity of habitat patches are closely linked to the other ecological processes discussed in this document. By definition, the presence of critical habitats (EP-1) determines patch pattern and connectivity (EP-2). Natural disturbance regimes (EP-3) are the major non-anthropogenic determinant of habitat patch patterns (the others being climatic and edaphic conditions). Similarly, hydrologic patterns (EP-5) can affect habitat patch pattern (as well as structural complexity EP-4) through flooding and stream scouring. The pattern of habitat patches such as wetlands may also affect nutrient cycling (EP-6) and purification services (EP-7). The connectivity of habitats patches (as opposed to fragmentation of habitat) has been shown to be critical to biotic interactions (EP-8) such as cowbird nest predation with consequences for interior-forest dwelling bird population dynamics (EP-9) and their genetic diversity (EP-10).

REFERENCES

Barrett, G.W. and P.J. Bohlen. 1991. Landscape ecology. In W.E. Hudson, ed. *Landscape Linkages and Biodiversity*. Defenders of Wildlife, Island Press, Washington, DC. pp. 149-161.

Comins, H.N. and I.R. Noble. 1985. Dispersal, variability, and transient niches: Species coexistence in a uniformly variable environment. *American Naturalist* 126:706-723.

Dramstad, W.E., J. D. Olson, and R.T.T. Forman. 1996. *Landscape Ecology Principles in Landscape Architecture and Land-Use Planning.* Harvard University, Graduate School of Design. Island Press, Washington, DC

Ewel, J.J. 1986. Ecosystem processes and the new conservation theory. In Pickett, S.T.A., R.S. Ostfeld, M. Shachak, and G.E. Likens, eds. 1996. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Diversity*. Chapman and Hall, New York.

Flather, C.H., S.J. Brady, and D.B. Inkley. 1992. Regional habitat appraisals of wildlife communities: A landscape-level evaluation of a resource planning model using avian distribution data. *Landscape Ecology* 7:137-147.

Harris, L.D. 1984. *The Fragmented Forest.* University of Chicago Press, Chicago, IL.

Harris, L.D. and G. Silva-Lopez. 1992. Forest fragmentation and the conservation of biological diversity. In P.L. Fielder and S.K. Jain, eds. Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management. Chapman and Hall, New York. pp. 197-237.

Hunter, M.L., Jr. 1996. *Fundamentals of Conservation Biology*. Blackwell Science, Cambridge, MA.

Levin, S.A. 1976. Spatial patterning and the structure of ecological communities. *Lecture on Mathematics in the Life Sciences* 81:1-35.

Levin, S.A. 1978. Pattern formation in ecological communities. In J.H. Steele, ed. *Spatial Pattern in Plankton Communities*. Plenum Press, New York. pp. 433-465.

MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

Noss, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.

Noss, R.F. 1991. Landscape connectivity: Different functions at different scales. In W.E. Hudson, ed. *Landscape Linkages and Biodiversity*. Defenders of Wildlife, Island Press, Washington, DC. pp. 27-39.

O'Neill, R.V., J.R. Krummel, R.H. Gardner, G. Sugihara, B. Jackson, D.L. DeAngellis, B.T. Milne, M.G. Turner, B. Zygmunt, S.W. Christensen, V.H. Dale, and R.I. Graham. 1988a. Indices of landscape pattern. *Landscape Ecology* 1:153-162.

O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner. 1988b. Resource utilization scales and landscape pattern. *Landscape Ecology* 2:63-69.

O'Neill, R.V., K.B. Jones, K.H. Riitters, J.D. Wickham, and I.A. Goodman. 1994. Landscape Monitoring and Assessment Research Plan. Environmental Protection Agency, Las Vegas, NV. EPA/620/R-94/009.

Paine, R.T. and S.A. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of patches. *Ecological Monographs* 51:145-178.

Paton, P.W.C. 1994. The effect of edge on avian nest success: How strong is the evidence. *Conservation Biology* 8:17-26.

Peters, R.L. and T.E. Lovejoy. 1992. *Global Warming and Biological Diversity*. Yale University Press, New Haven, CT.

Reid, T.S. and D.D. Murphy. 1995. Providing a regional context for local conservation action: A natural community conservation plan for the southern California coastal sage scrub. *BioScience Supplement* S-84-S-90.

Risser, P.G., J.R. Karr, and R.T.T. Forman. 1984. Landscape ecology: Directions and approaches. Special Publication No. 2. Illinois Natural History Survey, Champaign, IL.

Robbins, C.S., D.K. Dawson, and B.A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. *Wildlife Monographs* 103:1-34.

Soule, M.E., ed. 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK.

Spies, T.A., W.J. Ripple, and G.A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecological Applications* 4:555-568.

Stamps, J.A. 1991. The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology* 28:29-36.

Weins, J.A. and B.T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or landscape ecology from a beetle's perspective. *Ecology* 3:87-96.

Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone, In M.E. Soule, ed. *Conservation Biology*. Sinauer, Sunderland, MA. Pp. 237-256.

3. DISTURBANCE REGIME

DEFINITION

Ecosystems do not exist in a steady-state; they are dynamic, each possessing a characteristic composition, structure, and function that varies within limits over a course of tens to hundreds of years. Natural disturbance events, such as fires, floods, and wind, result in a significant change in ecosystem structure or composition. The natural disturbance regime of an ecosystem is the type, magnitude, and frequency of disturbances that would occur within the landscape in the absence of human activities.

WHAT CONSTITUTES A DISTURBANCE REGIME AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

At the landscape level, natural disturbances destroy patches of vegetation and restart plant succession. Examples of natural disturbances include fires, floods, droughts, wind storms, insect outbreaks, herbivory, beaver activity, and soil disruption by burrowing and trampling. These disturbances affect plant structure and community composition and may shape the dominant land forms in the landscape. "Disturbances are typically patchy in time and space, so that new disturbances occur in some portions of the stand or landscape while previously disturbed areas are recovering" (Noss and Cooperrider, 1994). An ever changing pattern of vegetation types and stages may determine the productive capacity of the ecosystem by (Pickett and White 1985, McNaughton et al. 1988, Pastor et al. 1988):

- changing the spatial and temporal patterns of nutrient availability,
- adding or removing biomass, and
- changing the ratio of live to dead material.

Ecosystems and species have adapted to habitat and disturbance conditions over long periods of time. Any deviation from these patterns or regimes can result in species losses or other undesirable ecological consequences. For example, disturbance creates microhabitats that provide the ideal conditions for plants and animals to thrive. The Kirtland's warbler requires a habitat created by disturbance (five- and six-year-old jack pines interspersed with grassy clearings) to successfully breed. This habitat is created and maintained by fires; certain species of pine (e.g., lodgepole pine, jack pine, and sand pine) require fire to regenerate because their cones open only with intense heat (Noss and Cooperrider 1994).

In addition to its importance to species, fire is integral to the function of many ecosystems (Ewel 1996). For example, fire greatly influences the cycling of nutrients, often increasing nutrient availability to immediate post-fire pioneer species. In regions where climate or nutrient availability limits the decay of woody debris, fire is a major agent of organic decomposition. In such situations, fire may be virtually inevitable with the frequency and behavior of wildland fire regulated by the rate and pattern of fuel accumulation(Christensen 1996).

Examples of other fire-dependant communities include prairies, other grasslands, oak savannas, ponderosa pine forests and longleaf pine forests. In general, fires and other disturbances allow for the regeneration and growth of trees and other plants. The patchiness created by these disturbances results in vertical and horizontal heterogeneity and a diversity in habitat types, adding to the productivity of the ecosystem.

Disturbance in the form of flooding is important in transporting materials needed to sustain many ecosystems. Bottomland hardwood forests, for instance, rely on periodic flooding to bring in water, particulate and dissolved organic matter, and nutrients. Flooding is also essential for exporting organic material from these forests for use in adjoining ecosystems and by their inhabitants. "When streams overflow into the bottomland, a large surface area of litter and detritus is exposed to the water, often for a long time. During this time, significant leaching and fragmentation occur, and both dissolved and particulate organic material are removed from the floodplain. Export of organic matter, therefore, follows seasonal, annual, or less-frequent hydrologic pulses" (Taylor et al. 1990).

HOW SHOULD THE DISTURBANCE REGIME BE DESCRIBED?

Each landscape possesses a characteristic natural disturbance regime that differs from other ecosystems in type, intensity, and timing. Disturbances can range from large stand-replacing disturbances, such as in western coniferous forests, to small patch disturbances, such as in eastern deciduous forests. It is critical in assessing environmental impacts to determine how the area affected by the proposed project fits into the natural disturbance regimes of the landscape. How will the project affect and be affected by the natural disturbance regime. Specifically, it is necessary to consider a large enough scale so that the cumulative effects of all relevant types of natural disturbance within the landscape are considered. This landscape-scale approach is also necessary to adequately consider ecological processes as discussed in Sections 1--Habitats Critical to Ecological Processes and 2--Pattern and Connectivity of Habitat Patches. Both the presence of critical habitat and the pattern of habitat patches are closely related to the natural disturbance regime in the landscape (Franklin and Forman 1987, Saunders et al. 1991).

To accurately assess a project's effects on natural disturbance regimes, the size of an area and the duration of impacts should be considered. Pickett and Thompson 1978 have defined the area needed to maintain a natural disturbance regime as the "minimum dynamic area". As theorized by Noss and Cooperrider (1994), "... a minimum dynamic area should be able to manage itself and maintain habitat diversity and associated native species with no human intervention." This concept is important in determining the scope of analysis and key considerations for evaluating potential impacts of projects. "Frequency analysis" can be used to predict the probability of natural disturbances occurring within a given amount of time. Historical records of natural disturbance (e.g., floods and hurricanes) are one of the best sources of frequency information, and they are available in many national and regional databases. Academic studies should be reviewed for past disturbances and their implications for ecosystem functioning. Disturbance history can also be obtained from soil cores, tree cores, and chronosequence studies (Johnson and Siccama 1989, Shortle et al. 1995). Changes in the concentrations of substances or in the variation of the soil horizons can indicate the sources of disturbance. Ecosystem reactions to past disturbance may be evidenced by a high incidence of disease or mortality, increase in proportions of r-strategists (organisms that produce a large number of young), or decrease in abundance or distribution of large organisms over time (Odum 1969).

HOW ARE DISTURBANCE REGIMES AFFECTED BY HUMAN ACTIVITIES?

Forests, rangelands, and aquatic ecosystems are all subject to natural disturbances of characteristic periodicities, return rates, and amplitudes. Fires, wind storms, and insect outbreaks are all important to forest dynamics, while fires and floods are most important in rangelands and river basins, respectively. Certain human activities (such as fire suppression, logging, grazing, and flood control) can have major impacts on these natural disturbance regimes, while others only peripherally affect disturbance patterns.

Land and water management actions are most likely to affect the natural disturbance regime. Well-designed programs may mimic the natural pattern to a certain extent; for example, silvicultural thinning by girdling mimics the stage in stand development when trees are fully occupying the site and competition between trees increases natural tree mortality (Oliver and Larson 1990). Forest management plans, however, commonly prescribe cutting forest stands at a rate faster than the natural disturbance frequency. Similarly, while domestic grazing patterns can mimic herbivory and trampling by native ungulates, they more often exceed the frequency and intensity of the natural disturbance regime, resulting in the decline of native grasses and invasion by exotic weeds. The invasion of exotic pests (e.g., bark beetles and gypsy moths) and diseases may accompany forestry management or agriculture practices (that result in monocultures) and effectively increase the frequency of disturbance in these ecosystems.

Whenever land and management plans change the extent and duration of a disturbance beyond the natural limits of the evolved disturbance regime, ecosystem composition, structure, and function can be adversely affected. Suppressed disturbances can lead to communities dominated by a few superior competitors, while extreme disturbance can lead to communities where only a few tolerant species can survive (Noss and Cooperrider 1994). Temporal changes in the phenology of components, the timing of pulses (fire or water flows), and species migrations (both local and long range) are all important. For example, lightening ignitions were once most common at the onset of the rainy season, when vegetation was still dry and the year's fires and convection storms appeared; in contrast, human-mediated ignitions are concentrated at very different seasons, either accidental ignitions during the midst of the dry season or prescribed burns during the cool season when wind and temperatures are best controlled (Ewel 1996).

Fire and flooding are the two most pervasive disturbance regimes affected by human activities. In both cases, either increases or decreases in the frequency, duration, and intensity of the disturbances can degrade ecosystems.

Fires. Fire is one of the most significant sources of natural disturbance in many parts of the world (Agee 1991, Specht 1991, Baker 1992). To varying degrees, Native Americans across North America regularly set fires, altering fire behavior and patterns of post-fire ecosystem development. In some cases, forests were replaced with grasslands through frequent burning to improve hunting, create agricultural fields, and support domestic animals. These fires varied geographically and over time and were likely influenced by changes in climate and cultures.

Today, the frequency of fires has increased in some and decreased in other forest and grassland systems beyond the range of variability experienced during this period or earlier pre-aboriginal times. Current human impacts on fire frequency and behavior include both (1) increased sources of ignition and (2) active fire suppression leading to fuel accumulation and fewer but higher-intensity fires (Christensen 1996). Human presence in fire-intolerant ecosystems can create more fires (through military activities, wildland recreation, and other sources) and more vulnerable vegetation (by altering hydrology and draining lands). Even a moderate increase in the incidence of fires may be followed by the invasion of insect pests, root pathogens, and competitively superior weeds.

Perhaps more common is the exclusion of fire that has altered many coniferous forests during the last 100 years. In these fire-dependent ecosystems, the vegetation has adapted to experiencing low-intensity fires at frequent intervals. Many plant species have adaptations to protect them from fires (thick, nonflammable bark, belowground burls and protected buds for rapid recovery), while others actually depend on fire for successful reproduction, (e.g., heat-stimulated cone opening of many pine species, germination in many chaparral shrub species, and flowering in many prairie and savanna species; Keeley 1981). The historical suppression of fires has caused fuel build-up that results in fires that are more intense than would normally occur. These intense fires damage the environment by destroying the soil organisms, taking upper story vegetation in addition to the lower canopy, destroying seeds, and shifting the competitive advantage from one species to another. When fire is absent from grassland and savannah ecosystems, the shift to woody vegetation can effectively exclude fire-adapted plants. In pine forests, the composition and age structure of tree species can change with repercussions for many species. A prominent example is how the practice of fire suppression in the jack pine forests of Michigan led to a shortage of young jack pine stands upon which the rare Kirtland's warbler depends (Probst and Weinrich 1993).

A dramatic example of the importance of maintaining natural fire regimes is the fire-dependent, long leaf pine-wiregrass ecosystem of the Gulf coastal plain (Noss and Cooperrider 1994). The natural disturbance regime is low-intensity ground fires recurring at intervals of 2 to 5 years. These fires burn downslope along elevational gradients to eliminate wetland shrubs that would otherwise move upslope. The burned areas produce an exceedingly species-rich, open herb-bog community of more than 100 herbaceous plants species (including pitcher plants, sundew, orchids) per acre (Clewell 1989). The natural disturbance of fire along this slope-moisture gradient form sandhills to wetlands is largely responsible for the many rare and endemic plant taxa in these communities. If fire is suppressed, biodiversity declines markedly.

Floods. Periodic flooding is the most important source of disturbance in riverine ecosystems; both inchannel habitats and riparian areas throughout the floodplain are affected. Human activities can dramatically alter the hydrology of an ecosystem (see Section 4--Hydrologic Patterns) in many ways, often changing the frequency, duration, or intensity of disturbance. As is the case with fire, flood frequency can be increased or decreased (as compared to the natural regime) by human activity. Commercial and residential development is ubiquitous on the landscape, as is the increase in flood frequency and intensity (flashiness) in nearby streams. Intense floods effectively "reset" the succession or development of aquatic communities more often than would occur naturally, benefitting invasive pioneering species over less tolerant natives.

Certainly the most dramatic, and also widespread, impact on flood regimes is the damming of streams and rivers. Not only are water supply and habitat quality affected by dams, but the natural disturbance regime of the downstream ecosystem (and the impoundment as well) is frequently altered. Run-of-the-river operations on dams are becoming more common, but flow manipulation for power generation is still the standard for most dams. Most of the time, dams reduce or eliminate flood-caused disturbances and diminish natural stream beach or riparian area replenishment. In the Missouri and Platte River systems the historical spring flood pulse has been greatly reduced, eliminating floodplain habitat for endangered species such as the piping plover and least tern.

In a highly visible attempt to partially return aspects of its natural disturbance regime to an important river system, Secretary of Interior Bruce Babbitt ordered release of large flood flows through the Glen Canyon Dam into the Colorado River and the Grand Canyon. Before the Colorado River was dammed, large floods pushed boulders from the downstream side of tributaries into the main channel, narrowing it and creating rapids. Below the tributary's mouth, circular eddies formed and the flood waters slowed, creating sandbars and calm backwaters after the flood subsided. Fishes native to this natural disturbance would ride out the flood against the side wall of the canyon where the velocity is lowest, while non-native species would be carried out in the mid channel. In this way new habitat would be created and new energy would enter into the ecosystem decaying vegetation and other organic matter trapped in the sediments was stirred up, liberating nutrients. The construction of the Glen Canyon dam, like many other western dams, disrupted this natural flood cycle causing sandbars to erode, backwaters to dry up, exotic fish species (such as catfish and carp) to invade (preying on and competing with native fish for food and spawning habitat), invasive plants (like tamarisk) to out compete native plants, and nutrients to remain locked in the sediments.

HOW CAN ADVERSE EFFECTS ON DISTURBANCE REGIMES BE MITIGATED?

Whenever land and water management plans affect how often, how long, and how intensely an ecosystem will be disturbed, the human-induced disturbance should fit within the natural limits of the evolved disturbance regime. The size of the area managed and the management options included should allow for these disturbance processes to function by allowing for the "...shifting mosaic of patches in various stages of recovery for disturbance" (Noss and Cooperrider 1994). In addition, mitigation of a specific project's impacts may be necessary to avoid alteration of disturbance patterns. Whenever possible, it is important to protect the attributes of disturbance regimes and the dynamic nature of ecosystems.

Using the example of fire disturbance, maintaining a fire-dependent ecosystem would include preserving the historic frequency of fires, intensity of fires, changes normally occurring during and after a fire, and the regeneration steps in the fire's aftermath. Mitigation could take the form of prescriptive burns in rotation over the area creating patches normally associated with that local environment. In the case of mitigation for altered flood regimes, dam operations should include releasing water (in appropriate amounts and durations) at appropriate times of the year to mimic natural flooding patterns. In some ecosystems, a landscape-level assessment of natural changes over time is needed. For example, the Atlantic white cedar Marconi Swamp in Massachusetts has been extremely dynamic over the last 1,000 years. Attempts to preserve existing stand structure may not approximate the normal character of the ecosystem. In such cases, a sufficient range of community types should be protected so that the disturbance of any particular site does not result in the areawide extirpation of its type.

In limited geographic areas, it may not be possible to include the full range of conditions as large scale disturbance might eliminate areas for recolonization. More intensive management may be necessary to maintain the necessary range of successional stages. Unless the area is very large, management may have to avoid the extremes of disturbance patterns. In some cases, a dilemma is created in letting nature take its course (e.g., with widespread fires or large floods) when the disturbance will directly eliminate or indirectly weaken species or communities in their last habitats (i.e., additional populations do not exist to recolonize the disturbed area because most of the suitable habitat area has been eliminated). The manager must decide how the rare species or communities should be saved while changing the natural disturbance regime which likely supports many other species and communities. A phased management approach could be taken, the rare species could be relocated, or implementation of management steps could be delayed. While letting nature take its course is most often beneficial for the ecosystem as a whole, a balanced effort should be made to meet all ecological objectives

Links between the disturbance regime and other ecological processes. The natural disturbance regime is closely linked to the other ecological processes discussed in this document. Hydrologic patterns (EP-5) are a major determinant of natural disturbances through flooding and stream scouring. All kinds of natural disturbances can affect the presence (EP-1) and pattern (EP-2) of certain habitat types, and more importantly the structural complexity (EP-4) of these habitats. As secondary effects, natural disturbances such as fire and windfall create organic debris that affect nutrient cycling (EP-6) and purification services (EP-7). Depending on the disturbance regime to which they are adapted, species population dynamics (EP-9), and secondarily their genetic diversity (EP-10) and biotic interactions (EP-8), can be very sensitive to natural and anthropogenic disturbances.

REFERENCES

Agee, J.K. 1991. The historical role of fire in Pacific Northwest forests. pp. 25-38. In: Walstad, J.D., S.R. Radoevich, D.V. Sandberg, eds. *Natural and Prescribed Fire in Pacific Northwest*

Forests. Oregon State University Press, Corvallis, Oregon.

Baker, W.L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73:1879-1887.

Christensen, N.L. 1996. Managing for heterogeneity and complexity on dynamic landscapes. In Pickett, S.T.A., R.S. Ostfeld, M. Shachak, and G.E. Likens, eds. 1996. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity*. Chapman and Hall, New York. pp. 167-186.

Clewell, A.F. 1989. Natural history of wiregrass. *Natural Areas Journal* 9:223-233.

Ewel, J.J. 1996. Ecosystem processes and the new conservation theory. In Pickett, S.T.A., R.S. Ostfeld, M. Shachak, and G.E. Likens, eds. The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity. Chapman and Hall, New York. pp. 252-261.

Franklin, J.F., and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecology* 1:5-18.

Johnson, A.H. and T.G. Siccama. 1989. Decline of red spruce in the high-elevation forests of the northeastern United States. pp. 191-243. In MacKenzie, J.J., M.T. El-Ashry, eds. *Air Pollution's Toll on Forests and Crops.* Yale University Press. New Haven, Connecticut.

Keeley, J.E. 1981. Reproductive cycles and fire regimes. In H.A. Mooney, T. M. Bonnickson, N.L. Christensen, J.E. Lotan, and W.A, Reiners, eds. Fire Regimes and Ecosystem Properties. U.S. Department of Agriculture Forest Service, Washington, DC. pp.231-277.

McNaughton, S.J., R.W. Ruess, S.W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* 38:794-800.

Noss, R.F., and A.Y. Cooperrider. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press, Washington, DC.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164:262-270.

Oliver, C.D., and B.C. Larson. 1990. *Forest Stand Dynamics*. McGraw-Hill. New York. 467 pp.

Pastor, J., R.J. Naiman, B. Dewey, P. McInnes. 1988. Moose, microbes, and the boreal forest. *BioScience* 38:770-777.

Pickett. S.T.A., and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves.

Biological Conservation 13:27-37.

Pickett, S.T.A. and P.S. White, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, New York.

Probst, J.R., and Weinrich. 1993. Relating Kirtland's warbler population to changing landscape composition and structure. *Landscape Ecology* 8:257-271.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18-32.

Shortle, W.C, K.T. Smith, R. Minocha, V.A. Alexeyev. 1995. Similar patterns of change in stemwood calcium concentration in red spruce and siberian fir. *Journal of Biogeography* 22:467-473.

Specht, R.L. 1991. Changes in the Eucalypt forests of Australia as a result of human disturbance. pp. 177-197. In: G.M. Woodwell, ed. *The Earth in Transition. Patterns and Processes of Biotic Impoverishment.* Cambridge University Press. Cambridge.

Taylor, J. R., M.A. Cardamone, and W.J. Mitsch. 1990. Bottomland Hardwood Forests: Their functions and Values. In J.G. Gosselink, L.C. Lee, and T.A. Muir. 1990. *Ecological Processes and Cumulative Impacts: Illustrated by Bottomland Hardwood Wetland Ecosystems*. Lewis Publishers.

4. STRUCTURAL COMPLEXITY

DEFINITION

At the local scale, ecosystems possess a natural complexity of physical features that provides for a greater variety of niches and more intricate interactions among species. Local structural complexity increases with more snags in the forest, more woody debris in the stream, and more shrubs in the desert. At other scales, spatial heterogeneity is equally important, affecting a wide range of ecological processes from predator-prey interactions to energy transfer among ecosystems.

WHAT CONSTITUTES STRUCTURAL COMPLEXITY AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

All ecosystems have physical features that increase the structural complexity of the environment. This structural complexity is a key factor determining its species diversity; ecosystems with more three-dimensional structure have more species (MacArthur and MacArthur 1961). For this reason, high structural complexity is most striking in biologically diverse ecosystems such as tropical forests and coral reefs. Both of these ecosystems possess vertical layers of structure in addition to intricate spaces in and around the living infrastructure (trees and corals). Vertical stratification in forests and aquatic systems usually involves stratification of light and temperature, as well as shelter and food sources. The structural complexity of natural streams can also be high when obstructions, substrates, and flow patterns have diversity in three dimensions. Considerable experimental evidence supports the concept that physical structure may prevent generalist foragers from fully exploiting resources and thus promote the coexistence of more species (e.g., Werner 1984). Simply put, complex habitats accommodate more species because they create more ways for species to survive (Norse 1990).

Research suggests that natural disturbance maintains structural complexity and that this complexity promotes plant and animal diversity (Hansen et al. 1991). In natural forests, the period between catastrophic disturbances is long enough to allow large trees, snags, and fallen trees to develop; many of these structures will also survive such events and continue to contribute to natural structural complexity. This structural complexity plays a critical role in the presence of the microclimate, food abundance, and cover that affect organism fitness (Cody 1985).

Dead trees are one of the most important contributors to increased structural complexity in forests and to the aquatic systems that receive them (Maser et al. 1988). Coarse woody debris creates new microhabitats and influences hydrology and nutrient cycling as it progresses from forests to streams and rivers and finally into estuaries. When a tree falls, the canopy is opened and additional light is admitted to the forest floor. The opening creates opportunities for new plants to become established. Fallen trees and branches suspended across other trees create elevated relief and structural complexity. The surface of the forest floor is roughened by fallen tree stems, their tipped rootballs, and the pits left after their uprooting. Fallen trees and branches provide a substantial reservoir of soil organic matter and essential nutrients increasing the chemical diversity of the forest.

Woody debris influences stream channel flow and creates foraging and rearing habitat for fish (Sedell et al. 1988). It creates critical substrate and cover for benthic invertebrates and amphibians. Debris accumulations generally increase pool frequency. Sediment stored by debris adds to the hydraulic complexity and creation of diverse microhabitats in streams. Large fallen trees can even be transported to estuaries where they support a variety of wood-degrading invertebrates (isopods and mollusks), as well as provide perches for eagles and haul out areas for seals (Gonor et al. 1988)

Coral reefs resemble rain forests in their biologically generated physical complexity; as with rain forests, this structural complexity contributes to high species diversity, elaborate specializations of component species, and coevolved associations among species (Reaka-Kudla 1997).Coral reefs support organisms in three major ecological roles: (1) suprabenthic fishes, (2) sessile epibenthic organisms that provide the complex structure of the reef (hard and soft corals, sponges, coralline and fleshy algae), and (3) the crypotfauna, including organisms that bore into the substrate as well as sessile encrusters and motile nestlers that inhabit bioeroded holes and crevices. On a larger scale, coral reefs provide physical ramparts that enclose lagoons and provide the primary nurseries and feeding grounds for fishes and other organisms. Even though coral reefs generally inhabit nutrient-poor waters, the complex ecological interactions made possible by their three-dimensional physical structure make them one of the most productive ecosystems in the world (Grigg et al. 1984).

Structural complexity is also important in more homogenous environments such as deserts. Even small amounts of physical structure can dramatically increase species diversity and ecological interactions. On the desert floor, "cryptogamic crusts" of nonvascular photosynthetic plants such as algae, lichens, and mosses support a microecosystem of bacteria, fungi, actinomycetes (as well as protozoans, nematodes, and mites). These crusts perform the critical functions of protecting soil from erosion, aiding in water infiltration, augmenting sites for seed germination, and increasing the soil's supply of nutrients (Klopatek 1992). Microtopographic features such as depressions or pits in the soil create environments for the collection of water and other resources that support shrubs or savanna vegetation. The benefits of spatial heterogeneity for biological diversity of deserts and other ecosystems continue along a scale gradient that ultimately includes landscape patch dynamics.

HOW SHOULD STRUCTURAL COMPLEXITY BE DESCRIBED?

Both live and dead organisms, generally plants, constitute the majority of structural diversity, although edaphic characteristics from stream bottoms to landforms contribute to physical structure. A large body of practice exists in forest ecology using random quadrat, line intercept, and point methods to determine the abundance and distribution of herbaceous and woody plants (Barbour et al. 1980). The measurement of structural complexity, however, usually focuses on the physical attributes rather than the identity of the organisms involved. For example, leaf area index, branch density, and vertical layer analysis can be measured in forests, as can quantities and dispersion of large woody debris (Whitaker 1975). Physical habitat measurement in streams has also been well studied, including application to indices for population estimates (Platts et al. 1983), minimum instream flows (Bovee 1982), and biological integrity (Rankin 1995). EPA's Rapid Bioassessment Protocols habitat assessment (Plafkin et al. 1989), Ohio's Qualitative Habitat Evaluation Index, and other methods focus on developing standard scores for physical parameters such as substrate quality, instream cover, channel quality, riparian quality, and pool/riffle quality. These parameters effectively describe the structural complexity of lotic ecosystems.

Old-growth forests represent structurally complex ecosystems with specific physical features that can be quantified. The following list of structural elements can be used to characterize the heterogeneous overall structure of forests, including multiple indistinct layers and much coarse woody debris (Norse 1990):

- uneven canopy with many gaps
- many trees with broken tops and cavities in trunks
- dominant trees with uneven heights and girths, often reaching greater maximums
- subcanopy trees of various heights
- uneven shrub, herb, and moss layers
- abundant epiphytes and perched soils on trunks and large branches
- uneven-size snags and logs with many logs in different stages of decay

Similar physical features are characteristic of the structurally complex streams found within undisturbed forested watersheds:

- many logs, including some large logs
- uneven stair-stepped gradient with pools common
- diverse sediments from silts to cobbles
- high overall habitat diversity

These qualitative and quantitative indicators of structural complexity within individual habitats are analogous to the concept of alpha diversity developed by Robert Whitaker (1975). By extension, complexity at larger scales can be considered analogous to beta (among habitats), and gamma diversity (among regions).

HOW IS STRUCTURAL COMPLEXITY AFFECTED BY HUMAN ACTIVITIES?

The most pervasive cumulative effect of past forest practices has been the reduction in structural complexity of forest habitats (Murphy 1995). A dramatic example is clearcutting, which by removing the moderating effects of the canopy and coarse woody debris, inevitably excludes many species. Even the selective logging of old-growth forests to produce even-aged stands and remove herbaceous vegetation dramatically reduces structural diversity. While a young forest or tree plantation may soon occupy the site, the exceptional structural complexity of the old-growth forest will diminish with the loss of deep crowns and diverse layers of understory trees; shrub-filled light gaps interspersed with densely shaded areas; furrowed bark and soil-covered branches; broken tops and epiphytes; and healthy, sick, and dead trees of different species (Noss 1990). In the southeastern United States, the creation of pine plantations has eliminated the old pines needed for nesting by red-cockaded woodpeckers and other species.

Hansen et al. (1991) speculate that even young, natural forests often have greater structural complexity than managed tree plantations. Managed forests have dramatically less structural complexity resulting from the clear-cutting of all trees and snags, prescribed burning or herbicide application to control competing vegetation, replanting with a single species, periodic thinning to maintain evenly spaced crop trees, and harvesting at 50-100 year intervals (Norse

1990). Although practices for wood production vary, managed plantations usually lack the multilayered canopy, diverse tree sizes, and abundant snags and fallen trees that exist in natural forests.

The removal of wood that would fall on the forest floor and into streams also reduces spatial heterogeneity. The lack of cover and soil compaction associated with logging can produce a 3.5-fold decrease in terrestrial amphibian (principally salamander) abundance (deMaynadier and Hunter 1995). Structural complexity in managed forest streams has declined primarily as a result of reductions in the size and frequency of pools following the filling with sediment and loss of large woody debris. This habitat simplification has caused a widespread reduction in salmonid diversity.

Reductions in stream structural complexity owing to agriculture (Schlosser 1982) and urbanization (Scott et al. 1986) have shown a similar pattern of decreased fish community diversity. The elimination of cobble interstices by sedimentation (reducing habitat heterogeneity) and the consequent loss of biotic integrity is a common result of increased runoff from impervious surfaces created by development. Channelization of streams during urban or agricultural development also alter the meander patterns and riffle-pool sequences that structure natural streams.

The natural structural complexity of estuarine and coastal shoreline environments has also been severely altered by human construction for habitation and commerce. Dredging and revetment (stone or concrete armoring) of shorelines eliminates the complexity of depths and diversity of microhabitats in the intertidal zone. Other relatively less complex natural environments such as grasslands and deserts still suffer important reductions in structural complexity. Natural grasslands with a high diversity of herbaceous plants flowering on a seasonal basis are replaced by cropland and pastureland uses with few (often introduced) species, reducing vegetation heights and near-soil structure. Desert floor "crustal communities" of cryptogamic plants and microphytic organisms also possess important structure at the microhabitat level that is lost when recreational and military vehicle activity convert the ground to homogeneous sands.

HOW CAN ADVERSE EFFECTS ON STRUCTURAL COMPLEXITY BE MITIGATED?

Mitigations for structural complexity are most important for the many forest management activities conducted in national forests and elsewhere, but the principles of retaining and restoring natural structural complexity hold for other environments as well. Logging practices that simplify the forest through clearcutting, thinning, or replanting with a limited number of species and ages should be restricted. Forest plans should address both species composition and age distribution, as well as the need to retain a natural disturbance regime that produces dead wood and diverse canopy structure. Most importantly, site preparation and logging practices that remove dead wood and other components of structural complexity should be done to restore the natural variability of that site.

Where vegetation management is required or desired it should be "messy." Virtually no natural disturbances create large bare patches like clearcuts; in all cases short of volcanic eruptions and meteor strikes, many nonliving structural elements and organisms remain after the disturbance as legacies vital to regeneration. Excessive neatness in logging practices eliminates the microhabitats that many species need. The larger the treatment, the more the manager should (1) cut in irregular shapes with feathered edges, (2) leave remnant patches of various sizes, and (3) leave adequate numbers of snags and logs so that the more disturbance-tolerant forest species can survive until surrounding conditions are suitable again.

In streams, practices such as channelization and simplification of habitat by concrete liners or bank stabilization structures should be discouraged. Alternatives to bulkheading and artificial bank stabilization that use natural materials such as rocks and woody debris should be employed to create or restore structural diversity to streams and shorelines.

In general all habitat manipulations should allow and encourage natural regeneration on some of the disturbed area. The proponent should plant a variety of species appropriate to the site, interspersed or in patches. For example, the adverse effects of logging on amphibian abundance can be mitigated, in some situations, by using regeneration practices that leave adequate microhabitat structure intact (deMaynadier and Hunter 1995).

Links between structural complexity and other ecological processes. Structural complexity is closely linked to the other ecological processes discussed in this document. It is a natural component of many critical habitats (EP-1) and on smaller scales is directly analogous to the landscape heterogeneity in the natural pattern of habitat patches (EP-2). Natural disturbance regimes (EP-3), such as fires and floods, are major determinants of structural complexity in forest (e.g., snags and fallen wood) and stream (e.g., scour holes) ecosystems. Structural complexity also may indirectly modify hydrologic patterns (EP-5) or contribute to nutrient cycling (EP-6) or purification services. As described above, complex physical heterogeneity (e.g., prey refuges) greatly influences biotic interactions (EP-8) among species and ultimate their population dynamics (EP-9) and genetic diversity (EP-10).

REFERENCES

Barbour, M.G., J.H. Burk, and W.D. Pitts. 1980. *Terrestrial Plant Ecology.* The Benjamin/ Cummings Publishing Company, Inc., Reading, MA.

Bovee, K.D. 1982. A Guide to Stream Habitat Analysis Using the Instream Flow Incremental Methodology. U.S. Fish and Wildlife Service Flow Information paper No. 12, FWS/OBS-82/26, Fort Collins, CO.

Cody, M.L. 1985. An introduction to habitat selection in birds. In M.L. Cody, ed. *Habitat Selection in Birds*. Academic Press, Orlando, FL.

deMaynadier, P.G. and M.L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: A review of the North American literature. *Environmental Review* 3:230-261.

Gonor, J.J., J.R. Sedell, and P.A. Benner. 1988. What we know about large tress in estuaries, in the sea, and on coastal beaches. In Maser et al, eds. From the Forest to the Sea: A Story of Fallen Trees. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. General Technical Report PNW-GTR-229.

Grigg, R.W., J.J. Polovina, and M.J. Atkinson. 1984. Model of a coral reef ecosystem. III. Resources limitation, community regulation, fisheries yield and resource management. *Coral Reefs* 3:23-27.

Hansen, A.J., T.A. Spies, F.J. Swanson, and J.L. Ohmann. 1991. Conserving biodiversity in managed forests. *BioScience* 41:382-392.

Klopatek, J.M. 1992. Cryptogamic crusts as potential indicators of disturbances in semi-arid landscapes. In McKenzie, D.H., D. E. Hyatt, and V. J. McDonald, eds. *Ecological Indicators*. Elsevier Applied Science, New York. pp. 773-786.

MacArthur, R.H. and J.W. MacArthur. 1961. On bird species and diversity. *Ecology* 42:594-598.

Maser, C., R.F. Tarrant, J.M. Trappe, and J.F. Franklin. 1988. From the Forest to the Sea: A Story of Fallen Trees. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. General Technical Report PNW-GTR-229.

Murphy, M.L. 1995. Forestry Impacts on Freshwater Habitat of Anadromous Salmonids in the Pacific Northwest and Alaska--Requirements for Protection and Restoration. NOAA Coastal Ocean Program Decision Analysis Series No. 7. NCAA Coastal Ocean Office, Silver Spring, MD..

Norse, E.A. 1990. *Ancient Forests of the Pacific Northwest*. Island Press, Washington, DC.

Noss, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.

Plafkin, J.L., M.T. Barbour, K.D. Porter, S.K. Gross, and R.M. Hughes. 1989. Rapid Bioassessment Protocols for Use in Streams and Rivers: Benthic Macroinvertebrates and Fish.

U.S. Environmental Protection Agency, Assessment and Watershed Protection Division, Washington, DC. EPA/444/4-89-001.

Platts, W.S., W.F. Megahan, and G.W. Minshall. 1983. Methods for Evaluating Stream, Riparian, and Biotic Conditions. General Technical Report No. INT-138. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Rankin, E.T. 1995. Habitat indices in water resource quality assessments. In Davis, W. and T. Simon (eds.) *Biological Assessment and Criteria: Tools for Water Resources Planning and Decision Making*. Lewis Publishers, Inc, Chelsea, MI. pp. 181-208.

Reaka-Kudla, M.L. 1997. The global biodiversity of coral reefs: A comparison with rain forests. In Reaka-Kudla, M.L., D.E. Wilson, and E.O. Wilson, eds. *Biodiversity II: Understanding and Protecting Our Biological Resources.* John Henry Press, Washington, DC.

Schlosser, I.J. 1982. Tropic structure, reproductive success, and growth rate of fish in a natural and modified headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences* 39:968-978.

Scott, J.B., C.R. Steward, and Q.J. Stober. 1986. Effects of urban development on fish population dynamics in Kelsey Creek, Washington. *Transactions of the American Fisheries Society* 114:555-567.

Sedell, J.R., P.A. Bisson, F.J. Swanson, and S.V. Gregory. 1988. What we know about large trees that fall into streams and rivers. In Maser et al, eds. From the Forest to the Sea: A Story of Fallen Trees. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. General Technical Report PNW-GTR-229.

Werner, E.E. 1984. The mechanisms of species interactions and community organization in fish. In Strong, D.R., Jr., D. Simberloff, L.G. Abele, and A.B. Thistle. Ecological Communities: Conceptual Issues and the Evidence. Princeton University Press, Princeton, NJ. pp. 360-382.

Whitaker, R.M. 1975. *Communities and Ecosystems*. Second Edition. Macmillan, New York.

5. HYDROLOGIC PATTERNS

DEFINITION

Ecosystems possess natural hydrologic patterns that provide water for organisms and physical structure for habitats. This cycle of water is also the vehicle for the transfer of abiotic and biotic materials through the ecosystem. The natural hydrologic patterns of an ecosystem include the magnitude, frequency, duration, timing, and rate of change (flashiness) of water flow.

WHAT CONSTITUTES A HYDROLOGIC PATTERN AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

Water is essential as sustenance for organisms and as a driving force for physical changes to the environment. It also serves to transport energy, nutrients, and biota themselves. To understand the biodiversity, production, and sustainability of ecosystems, it is necessary to appreciate the central role of dynamically varying physical environments. Hydrologic patterns in aquatic ecosystems and their surrounding landscapes play a key role in these dynamics.

Aquatic ecosystems, primarily wetlands, streams, and rivers, are totally dependent on hydrology. The terrestrial components of watersheds, especially riparian areas, are heavily influenced by hydrology. River inflow and tidal patterns also help shape estuarine and marine ecosystems. Water provides an interconnectedness among ecosystems that is critical to understanding regional ecological functioning. The concept of water as an integrator of conditions upstream has been used to develop methods for resource management (e.g., EPA's watershed approach), but it is not only the amount and direction of water flow that is important but also the variability in flow.

The range of hydrologic variability in streamflow quantity and timing can be thought of as a "master variable" affecting biodiversity and ecological integrity in riverine systems. The natural flow of a river varies on a time scale of days, seasons, years, and longer (Poff et al. 1997). This variability is the result of the cycle of evaporation, precipitation, and infiltration or runoff into waterbodies. The amount and timing of flows downhill carry nutrients, sediment, pollutants, dead wood, and organisms to larger streams and ultimately to lakes or estuaries.

There are five critical components of the flow regime (Poff and Ward 1989, Richter et al. 1996):

- magnitude
- frequency
- duration
- timing
- rate of change (flashiness) of hydrologic conditions

These components interact to maintain the dynamics of inchannel and floodplain habitats that are essential to aquatic and riparian species (Poff et al. 1997). The natural flow regime reflects regional variation in climate, geology, topography, soils, and vegetation, and is closely tied to specific geomorphic processes and ecological functions. Broad regional signatures of the interactions among these components of flow regime can be identified, as in the case of constrained canyon segments versus unconstrained alluvial segments within the floodplain (Poff et al. 1997). In any case, the effects of changes in the natural flow regime are invariably location dependent.

Magnitude, frequency, and duration of high and low flows. Minimum and maximum flows over different time intervals are commonly used to characterize natural hydrology. These and other aspects of flow regime dynamics are important because they often act as ecological "bottlenecks" (i.e., critical stresses or opportunities) for riverine species (Poff and Ward 1989). There are many reasons why the magnitude and frequency of high and low flows affect ecological processes.

High flows may transport sediment through the channel and kill or displace benthic invertebrates; at the same time, these flushing flows clean out gravel beds of accumulated silt and provide sites for attachment of insect eggs and other organisms. They import woody debris, creating new habitat. High overbank flows connect channels to floodplains, increasing overall productivity and diversity. The scouring of floodplains rejuvenates habitat for plant species. Low flows may determine the amount of habitat available in the channel during critical periods. In some systems, temporary drying of stream channels provides habitat for specialized species.

The durations of high and low flows also critically affect natural communities. Specifically, prolonged inundation is often the most important source of mortality among riparian plants (Chapman et al. 1982). Mortality can also occur during low flow as a result of high temperatures and low dissolved oxygen levels or from very cold temperatures and ice scour (Schlosser 1990).

Timing or predictability of flow events. The timing of flows is also critical to ecological integrity, because many species are adapted to avoiding or exploiting natural high and low flows for spawning, egg hatching, rearing, feeding, or reproduction. Access to the floodplain during these events, or the ability to make upstream and downstream migrations, is especially important. Plants, in particular, are adapted to the seasonal timing of flow events through "emergence phenologies" that determine the sequence of flowering, seed dispersal, and seedling growth (Poff et al. 1997).

Rate of change or flashiness. In addition to the timing or predictability of flow events, the rate of change of flow, or flashiness (rapid rises in flow), is important to ecological integrity. The native desert fishes of the Southwest are adapted to historically flashy conditions. These native fishes have adapted to avoid being displaced downstream by the rapid onset of floods while nonindigenous species have not. Where gradual drying in seasonal streams is the natural condition, native aquatic fishes are able to emigrate safely, and native riparian plants can effectively establish themselves. In many other stream systems, only moderate fluctuations in the flow regime are natural, and native species are not adapted to flashy conditions.

While the role of natural hydrologic patterns are most important for riverine and wetland ecosystems, the dynamics of ocean tides and storm flows are also driving forces behind the structure of high energy (i.e., beach) coastal ecosystems (Pilkey and Dixon 1996). On coastal plains (low flat surfaces such as the Gulf of Mexico and Atlantic), rising sea level, a large supply of sand, and large waves combine to form barrier islands. As sea level rises, islands migrate toward the mainland as they roll over themselves. Over that last century or two, barrier islands that were stable or widening over the prior four thousand years have begun to narrow in response to erosion on all sides (probably in response to sea level rise). On beaches, winds, waves, and storms keep sand in constant motion, producing the largest movement of sand in "longshore currents." These currents, or littoral drift, cause sand to move downdrift along the beach. In the absence of human efforts to protect shorefront buildings, natural coastal hydrology will move sand downdrift and either landward or seaward in a dynamic equilibrium that maintains coastal beaches.

HOW SHOULD HYDROLOGIC PATTERNS BE DESCRIBED?

Quantitative assessments of the critical components of the flow regime can be obtained from stream gage records maintained by the U.S. Geologic Survey or other institutions. Richter et al. (1996) have recently developed a method for assessing hydrologic alteration attributable to human influence with ecosystems. This method analyzes hydrologic data from stream gages (or other point data such as wells) or from model-generated data using 32 "Indicators of Hydrologic Alteration" that describe ecologically significant features of surface and groundwater regimes. These indicators effectively characterize hydrologic patterns in the following five groupings: magnitude, magnitude and duration of annual extreme conditions, timing of annual extreme conditions, frequency and duration of high and low pulses, and rate and frequency of change in conditions. The central tendency and dispersion of these indicators under natural (i.e., reference or pre-impact) flow regimes can be used (1) to determine the deviation caused by dam operation, flow diversion, groundwater pumping, and intensive land-use conversion or (2) to set streamflow-based river ecosystem management targets based on the "Range of Variability Approach" (Richter et al. 1997).

In addition, several techniques for inferring hydrologic patterns from evidence of channel impacts have been developed, including the Rapid Bioassessment Protocols (RBPs) habitat assessment (Plafkin et al. 1989) and the Rosgen geomorphological river classification (Rosgen 1994). The RBP habitat assessment is based on visual estimates of habitat features and uses subjective scoring of a dozen parameters on a standard scale. Many other methods using a similar approach have been developed and customized for selected regions (Rankin 1995). Each method includes parameters that reflect changes in the hydrologic pattern such as bank erosion and embeddedness. David Rosgen (1994) developed a different approach by describing the physical appearance and character of a river as a product of the adjustment of the river boundaries to the current streamflow and sediment regime. Rosgen's seven major classes of streams reflects differences in entrenchment, gradient, width-depth ratio, and sinuosity in various landforms. This and related methods are being used to evaluate the effects of altered hydrologic patterns and to plan restoration efforts.

HOW ARE HYDROLOGIC PATTERNS AFFECTED BY HUMAN ACTIVITIES?

Human induced changes in any of the five components of the natural flow regime can dramatically affect ecosystems. For example, the extreme daily variations from peaking power hydroelectric dams have no natural analog and thereby usually reduce the natural diversity and abundance of a wide range of fishes and invertebrates. In contrast, flow stabilization below water supply reservoirs results in artificially constant environments, eliminating species adapted to natural dynamics. Even tolerant species cannot withstand water withdrawals for municipal, industrial, and agricultural uses that fail to provide minimum flows.

The Nationwide Rivers Inventory (National Park Service 1996) has determined that less than 2% of the estimated 3.25 million river and stream miles in the United States (excluding Alaska and Hawaii) possess the significant natural and cultural attributes to qualify for the national Wild and Scenic River System, primarily because of dams and other major hydrologic modifications. Obviously, structures such as dams and levees directly alter hydrology by constraining the flow of the river and creating impoundments. The degree to which flows are changed depends on the management regime of the facility. Run-of-the-river operations on dams are becoming more common, but flow manipulation for power generation is still the standard for most dams. Discharges from hydroelectric dams may strand individuals in unfavorable habitats, or displace them downstream, by increasing flashiness or altering the seasonal timing of pulsing flows. In recent years, the rate of large dam construction has slowed and flood control projects have been reassessed. Nonetheless, there are many opportunities to reevaluate the impacts of existing dams undergoing regulatory relicensing and to develop effective mitigations to facilitate the recovery of endangered species and the reestablishment of sustainable fisheries.

In addition to periodic high flow discharges, hydroelectric dams and other reservoir systems alter natural flow regimes by instituting more regular, lower flows and reducing flushing of sediments. By reducing flashiness, these systems adversely affect species such as the Pecos bluntnose shiner and cottonwood that are competitively superior in flashy regimes. In general, naturally variable streams and rivers appear more resistant to invasion by lake-inhabiting species (Moyle and Light 1996). For example, in the Southwest, rivers where exotic fish species are reduced periodically by natural flash floods are often the last stronghold of native endemics (Minckley and Deacon 1991). In addition, less flashy regimes decrease overbank flows, degrading riparian communities through desiccation, ineffective seed dispersal, and poor plant establishment. For example on the Platte River, the loss of physical scouring eliminates nesting habitat for species such as the piping plover and least tern, shifting the faunal composition from one characteristic of large prairie rivers to one typical of the cosmopolitan forested regions of the eastern United States (Knopf and Scott 1990). Even when floods continue, the timing of flood events is critical. When the timing of floods is artificially changed, exotic plant species with less specific gemination requirements (e.g., salt cedar) may invade (Horton 1977). Wootton et al. (1996) showed that the entire food web structure of northern California rivers changed when off-season floods were introduced by dam operations as a result of high mortality among important consumer species in vulnerable life stages.

Even without dams, stream flow can increase as the amount of impervious surface expands during land development for commercial and residential uses. Impervious surfaces prevent infiltration and direct water away from subsurface pathways to overland flow, increasing the flashiness of streams. Urbanization and suburbanization commonly exceed the threshold of approximately 10% to 20% impermeable surface that is known to cause rapid runoff throughout the watershed (Center for Watershed Protection 1994). In heavily urbanized watersheds, stream channelization and large amounts of impervious surface result in rapid changes in flow, particularly during storm events. These artificially high runoff events increase flood frequency (Beven 1986), cause bank erosion and channel widening (Hammer 1972), and reduce baseflow during dry periods. These modifications of natural hydrologic patterns are perhaps the most pervasive effects of human activities.

Agricultural practices also greatly affect hydrologic patterns. Clearing forest and prairie environments generally decreases interception of rainfall by natural plant cover and reduces soil infiltration, resulting in increased overland flow, channel incision, floodplain isolation, and headward erosion of stream channels (Prestegaard 1988). Draining and channelizing wetlands directs flow more quickly downstream, increasing the size and frequency of floods, and reducing baseflow. Such activities can actually increase the magnitude of extreme floods by decreasing upstream storage capacity and accelerating water delivery. In 1993, the catastrophic floods along the Mississippi River resulted from levee failures as high flows (created by reduced upstream storage) sought to reestablish river connections to the floodplain.

Water withdrawal is a less ubiquitous, but obviously important, factor affecting hydrologic patterns. Withdrawals and diversions of water can eliminate streams, reduce habitat, or impoverish vegetation by lowering groundwater levels. Small municipal water withdrawals may go unnoticed, but can severely affect small streams. Lowering groundwater levels can degrade caves and subterranean systems, as well as dry out headwater streams and vernal pools. Ditching and diversion of water on small agricultural plots or as part of huge water redirection systems like those in South Florida can completely change the hydrology of adjacent ecosystems. The cascade of effects on vegetation and endangered species in the Everglades and Florida Bay resulting from diverting the "river of grass" to coastal cities is the focus of a national ecosystem restoration effort (CEQ 1993).

Alteration of natural hydrologic patterns in coastal environments is also common, often with devastating results for human activities and natural ecosystems. Barrier islands, perhaps the most dynamic coastal ecosystems, are also the center of conflict between the demand for beachfront development and migration of beaches as a result of natural hydrologic forces (Pilkey and Dixon 1996). On coastal plain coasts with rising sea level (the dominant pattern over the last 100 to 200 years), a large supply of sand, and large waves, barrier islands migrate toward the mainland as the they roll over themselves. This shoreline erosion in fundamentally the ocean nibbling away at the edges of the continent. Most estimates indicate that 80 percent or more of the United States shoreline is eroding. Although climate-related sea level rise, land subsidence, and other factors influence this process, most often local erosion is the result of human activity. Seawalls, jetties, groins, breakwaters, navigation channels, deepening, inlet formation, and sand removal by mining all contribute to shoreline retreat. By interrupting the hydrological forces that supply sediment to beaches, all effective shoreline engineering procedures create erosion. While very effective for protecting shorefront property from shoreline erosion, seawalls also destroy beaches. Some beach is lost by the actual shoreward location of the seawall (placement loss); more importantly the wall is a barrier against which retreating beaches narrow and ultimately disappear (passive loss); and lastly the wall itself may intensify wave actions and the (active) loss of beach sand. Offshore engineering solutions such as breakwaters, groins, and jetties directly affect the longshore currents, or littoral drift, that move sand downdrift along the beach (usually southerly on the Atlantic coast, but varying by location and season). This natural river of sand is disrupted when humans build structures that interrupt water flow. As with a dam, building a groin or jetty on the beach, perpendicular to the shoreline, will interrupt longshore current and cause sand to deposit updrift and erode downdrift.

HOW CAN ADVERSE EFFECTS ON HYDROLOGIC PATTERNS BE MITIGATED?

The natural hydrologic pattern is important for maintaining the form of the channel and floodplain, habitat heterogeneity, ecosystem productivity, and biodiversity. This means that mitigation measures need to ensure not only the continued flow of a specified quantity of water, but also the natural variability in flow.

Historically, mitigation has focused on meeting minimum flow requirements for selected species confined to the wetted river channel. Approaches have ranged from best professional judgement to the Instream Flow Incremental Methodology (IFIM)(Bovee and Milhous 1978), which couples physical habitat preferences of fishes with how habitat availability varies with discharge. The statistical and biological assumptions of IFIM have been criticized (Baringa 1996, Poff et al. 1997), but more importantly, such approaches ignore the fact that what is good for the ecosystem need not consistently benefit individual species and vice versa. Some species benefit more during wet years, some during dry years, and overall biodiversity and ecosystem functioning benefit from interannual variation in species success (Tilman et al. 1994). In addition, the consequences of naturalizing a flow regime for individual species cannot be predicted with high certainty because of interaction with other species (Wootton et al. 1996).

For these reasons, although IFIM is a potentially useful tool for evaluating the effects of altering flow, many situations will require a broader look at multiple aspects of hydrologic regimes. Analysis of the hydrologic record can yield greater understanding of flow conditions for a particular system (Richter et al. 1996), providing an opportunity to examine the magnitude, frequency, duration, timing, and predictability of flows. In systems already subject to hydrologic modification, data from both historical (pre-impact) and recent (post-impact) times can be compared. The best method may be to use holistic and qualitative approaches in concert with quantitative and reductionist approaches. Poff et al. (1997) conclude that "attempting to engineer optimal conditions for all species at once is not possible, whereas a holistic view that allows for natural environmental dynamics and subsequent year-to-year variability in species success and ecological processes can provide for long-term success." It is difficult to develop specific criteria for flow mitigation because the understanding of flow components with geomorphic and ecological processes is imperfect; therefore, experimental and adaptive management should be favored. Standards should be river specific. The "Range of Variability Approach" (Richter et al. 1997) using Indicators of Hydrologic Alteration has the potential to effectively quantify streamflow-based management targets for individual rivers.

Future impacts can be evaluated with the goal of minimizing, when and where possible, alterations of natural flow regimes, while mitigation measures can be designed to protect or restore natural hydrologic patterns, particularly at the most ecologically critical times. For example, dam releases can be timed to restore spring high-flow pulses to provide flushing and natural accretion of sandy sediments to feed downstream beaches. In other systems, discharges may be managed to maximize habitat availability during critical spawning periods for fish. In urban systems, stormwater best management practices (BMPs) can be employed to reduce direct inputs of flow from upland sources. Water withdrawals can be restricted to maintain inchannel flows, particularly during low flow seasons or in areas identified as important wildlife or fish habitat. Maintaining natural wetlands near rivers allows for the uptake of excess water during high rainfall periods and for slow release after storms. In some situations, restoring stream channel morphology, and reconnecting the river to its natural floodplain, can help reestablish the river's ability to handle flow and sediment loads. Such efforts should be undertaken with an understanding of fluvial processes and the circumstances affecting a particular river system. In cases where river systems have been substantially altered (e.g., where restoration of overbank flooding is impossible), mitigation can attempt to simulate geomorphic processes. In Boulder Creek, Colorado, clearing of selected vegetation to expose sediments and well-timed irrigation have substituted for flood flows in enhancing cottonwood recruitment (Friedman et al. 1995).

Pilkey and Dixon (1996) discuss at length the implications of the various shoreline armoring "solutions" undertaken by the U.S. Army Corps of Engineers and others to deal with dynamic coastal ecosystem hydrology. They conclude that there is no compromise between saving shorefront property and maintaining the beach. Shoreline armoring inevitably is irreversible and leads to larger and higher structures and the loss of the beach. Beach replenishment is a better solution, but one that is very costly and only temporary as the beach will soon be lost again. Moving the buildings is the only environmentally effective solution, one used before engineering solutions began. From the point of view of minimizing environmental effects, development of shores with inevitable modifications of coastal hydrology should be avoided.

Links between hydrologic patterns and other ecological processes. The hydrologic patterns of an ecosystem are closely linked to other processes discussed in this document. The presence of water in adequate amounts and durations ultimately determines the extent of wetlands, one of the habitats critical to ecological processes (EP-1). The networks of waterbodies also provide one of the most important forms of connectivity among habitat patches (EP-2). The discussion in this section of the importance of variability in flow regimes essentially focuses on hydrology as an agent of natural disturbance (EP-3). The transport and scouring of aquatic habitat affects structural diversity (EP-4) and carries nutrients downstream (EP-6). The amount of flow is important for assimilating and purifying waste inputs (EP-7). Lastly, hydrology is one abiotic component of ecosystems influencing the degree to which biotic interactions structure aquatic communities (EP-8).

REFERENCES

Baringa, M. 1996. A recipe for river recovery? *Science* 273:1648-1650.

Beven, K.J. 1986. Hillslope runoff processes and flood frequency characteristics. In Abrahams, A.D., ed. *Hillslope Processes*. Allen and Unwin, Boston, MA. pp.187-202.

Bovee, K.D. and R. Milhous. 1978. Hydraulic simulation in instream flow studies: Theory and techniques. Instream Flow Information Paper No. 5, FWS/OBS-78/33. U.S. Fish and Wildlife Service, Fort Collins, CO.

Center for Watershed Protection. 1994. The importance of imperviousness. *Watershed Protection Techniques* 1:100-111.

Chapman, R.J., T.M. Hinckley, L.C. Lee, and R.O. Tesdey. 1982. Impact of water level changes on woody riparian and wetland communities. Vol. 10. U.S. Fish and Wildlife Service OBS-82/23.

Council on Environmental Quality (CEQ). 1993. Environmental Quality: The Twenty-fourth Annual Report of the Council on Environmental Quality. Executive Office of the President, Washington, DC.

Friedman, J.M., M.L. Scott, and W.M. Lewis, Jr. 1995. Restoration of riparian forest using irrigation, artificial disturbance, and natural seedfall. *Environmental Management* 19:547-557.

Hammer, T.R. 1972. Stream channel enlargement due to urbanization. *Water Resources Research* 8:1530-1540.

Horton, J.S. 1977. The development and perpetuation of the permanent tamarisk type in the phreatophyte zone of the Southwest. USDA Forest Service General Technical Report RM-43:124-127.

Knopf, F.L. and M.L. Scott. 1990. Altered flows and created landscapes in the Platte River headwaters, 1840-1990. In J.M. Sweeney, ed. *Management of Dynamic Ecosystems.* The Wildlife Society, West Lafayette, IN. pp. 47-70.

Minckley, W.L. and J.E. Deacon, eds. 1991. *Battle Against Extinction: Native Fish Management in the American West.* University of Arizona Press. Tucson.

Moyle, P.B. and T. Light. 1996. Fish invasions in California: Do abiotic factors determine success? *Ecology* 77:1666-1669.

National Park Service. 1996. The Nationwide Rivers Inventory. CD-ROM prepared by the U.S. Geological Survey and other federal agencies for the National Park Service, Washington, DC.

Pilkey, O.H. and K.L. Dixon. 1996. *The Corps and the Shore*. Island Press, Washington, DC.

Plafkin, J.L., M.T. Barbour, K.D. Porter, S.K. Gross, and R.M. Hughes. 1989. Rapid Bioassessment Protocols for Use in Streams and Rivers: Benthic Macroinvertebrates and Fish. U.S. Environmental Protection Agency, Washington, DC. EPA/440/4-89/001.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime: A paradigm for river conservation and restoration. *Conservation Biology*: under review

Poff, N.L. and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.

Prestegaard, K.L. 1988. Morphological controls on sediment delivery pathways. In Walling, D.E., ed. Sediment Budgets. International Association of Hydrological Sciences Publication No. 174. IAHS Press, Wallingford, UK. pp. 533-540.

Rankin, E.T. 1995. Habitat indices in water resource quality assessments. In Davis, W. and T. Simon (eds.) *Biological Assessment and Criteria: Tools for Water Resources Planning and Decision Making*. Lewis Publishers, Inc, Chelsea, MI. pp. 181-208.

Richter, B.D., J.V. Baumgartner, J. Powell, and D.P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* 10:1163-1174.

Richter, B.D., J.V. Baumgartner, R. Wigington, and D.P. Braun. 1997. How much water does a river need? Freshwater Biology 37.

Rosgen, D.L. 1994. A classification of natural rivers. *Catena* 22:169-199.

Schlosser, I.J. 1990. Environmental variation, life history attributes, and community structure in stream fishes: Implications for environmental management assessment. *Environmental Management* 14:621-628.

Tilman, D., J.A. Downing, and D.A. Wedin. 1994. Does diversity beget stability? *Nature* 371:257-264.

Wootton, J.T., M.S. Parker, and M.E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558-1561.

6. NUTRIENT CYCLING

DEFINITION

Ecosystems have evolved efficient mechanisms for cycling nutrients, which combined with sunlight and water determine the productivity of the system. The natural flow of organisms, energy, and nutrients is essential for maintaining the trophic structure and resiliency of the ecosystem. Reduction or augmentation of nutrient inputs to ecosystems can drastically alter these trophic interactions and ultimately the quality of the environment. The input and assimilation of nitrogen is the most common measure of nutrient cycling, but the dynamics of other essential compounds are also important.

WHAT CONSTITUTES NUTRIENT CYCLING AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

Nutrient cycles are the processes by which elements such as nitrogen, phosphorus, and carbon move through an ecosystem. This cycling is critical to the functioning of ecosystems; otherwise essential elements and nutrients would continue on a relentless flow downhill, depleting ecosystems uphill (Noss and Cooperrider 1994). But terrestrial and aquatic systems have developed mechanisms that slow the movement of water, nutrients, and energy to the sea. Vegetation of all types intercepts nutrient-rich waters and bind materials in place. Anadromous fishes and other migrating species move major amounts of biomass and minerals upstream, but the role of animals in moving nutrients uphill has received relatively little study.

Historically, ecosystem studies have focused on the transfer of nutrients and energy among the various components of the biotic and abiotic environment (Odum 1971). Many aspects of organismal ecology are also based on the importance of nutrients for species growth and survival. Because nutrients often set the limits of primary or secondary productivity of populations and communities, research for agriculture in forestry usually concentrate on the use of fertilizers to supplement nutrient levels. As with all ecological processes, when the natural level or flow within the ecosystem is changed (either increased or decreased), ecological integrity is degraded.

Ecosystems are not isolated from one another; nutrients come into and out of ecosystems via meteorological, geological, and biological transport mechanisms (Krebs 1978). Meteorological inputs include dissolved matter in rain and snow, atmospheric gases, and dust blown by the wind; geological inputs include elements transported by surface and subsurface drainage; and biological inputs include movement of animals between ecosystems. Nutrient cycles can be divided into two broad types: sedimentary or local cycles that operate within an ecosystem (e.g., phosphorus in a lake) and gaseous or global cycles (e.g. nitrogen, carbon, oxygen, and water across landscapes and regions).

Trophic interactions within ecosystems (e.g., the food chain of plant-herbivore-carnivore) are the most visible part of the cycling of energy and nutrient within ecosystems. Changes in the input or export of nutrients within ecosystems can affect the status of these trophic levels and can have ramifications for biotic interactions as well as ecosystem functioning. Less obviously, decomposers (such as invertebrates and microorganisms) serve the critical role of recycling dead material at each stage of the nutrient cycle and ultimately supply the soil nutrients that feed the plants that capture the sun's energy.

Soils are a key factor regulating element and nutrient cycles. The amount of carbon and nitrogen in soils is much greater than that in vegetation, 2 to 20 times respectively (Daily et al. 1997). Soil consumes wastes and the remains of dead organisms and recycles their constituent materials into forms usable by plants. In the process, soil organisms regulate the fluxes of carbon dioxide, methane, and nitrogen oxides in the atmosphere.

Plants require 21 essential elements that, along with water, determine growth (Vogt et al. 1997). Plants acquire nutrients from soil exchange sites, soil weathering, above- and below-ground litter that is decomposed by soil fauna and flora, and internal retranslocation within the plant tissues. In most forests ecosystems, tree growth is constrained by one or more of the following nutrients: nitrogen, phosphorus, potassium, calcium, or magnesium (Lassoie and Hinckley 1991). Fixation of atmospheric nitrogen by certain soil bacteria and blue-green algae is critical to the productivity of many terrestrial and aquatic ecosystems.

Large rivers, estuaries, coastal waters, and especially lakes have evolved to process of nutrient inputs within a specific range. In general, the nutrient base of these ecosystems comes from producers using solar energy. Excessive nutrient loadings result in eutrophication, the enrichment of waters by a previously scarce nutrient. During eutrophication, algae and cyanobacteria grow unchecked and their subsequent decomposition robs the water of oxygen, reducing or eliminating populations of fish and other aquatic species. Conversely, many smaller streams have a nutrient base of leaves and downed wood that feeds insects shredders and collectors. When this nutrient base is diminished by the removal of downed wood or logging of forests, production rapidly declines. Forest and grassland ecosystems are wedded to the richness of their soils and may decline in health or transform into other vegetative communities as they lose nutrients through soil erosion or leaching. Nutrients that usually cycle between vegetation and soils may also be lost during severe insect infestations (Swank 1988).

HOW SHOULD NUTRIENT CYCLING BE DESCRIBED?

Nutrient cycling is one of the biogeochemical cycles that is best described in a diagram consisting of different compartments (Krebs 1978). A compartment contains a certain quantity, or pool, of nutrients. In a simple lake ecosystem, the phosphorus dissolved in the water is one pool and the phosphorus contained in herbivores is another pool. Analysts measure the exchange of nutrients between compartments as the flux rate. Increasingly elaborate models of nutrient cycling can be developed depending on the knowledge of the specific ecosystem under study. The more accurate the model, the more precise can be the threshold of change leading to degradation of the ecosystem.

Nutrient cycles can be studied by introducing radioactive tracers into laboratory or natural ecosystems. Results of laboratory studies provide mechanistic explanations for dynamics that are critical for understanding the status and trends of affected ecosystems. For example, phosphorus and other nutrients tend to accumulate in the sediment of lakes so that productivity depends on continual nutrient inputs. Measurement of nutrients in both the water column and sediment are important for understanding the effects of excessive nutrient inputs and eutrophication.

Studies on plant nutrition have shown that nitrogen is the most limiting nutrient in many ecosystems. Changes in nutrient cycling can be assessed by visual inspection of plant condition, chemical analysis of leaf tissues, and soil analysis of nutrient availability (Vogt et al. 1997). Because nitrogen is a dominant factor in nutrient cycling, easily measurable and sensitive parameters that are mechanistically related to nitrogen effects may be especially useful for understanding the connections between ecological processes at different scales.

Documenting nutrient uptake and cycling in ecosystems is a valuable tool for managers. The fastest and easiest approach uses visual appearance to identify symptoms indicating nutrient deficiencies (assuming that the confounding effects of fungal disease, insect attacks, drought, pesticides, or air pollution can be overcome). A more quantitative and precise method is chemical analysis of leaf tissue to determine mineral nutrition (again, the confounding effects of interactions among different nutrients, genetic differences among individuals, and environmental influences must be considered). Another way to analyze nutrient relations is to assess the availability of nutrients in the soil. It is important to note that the nutrient content of the soil may not accurately reflect availability for uptake by plants and that plant-mycorrhizal associations often play an important role. A leaf's photosynthetic capacity is strongly correlated to its nitrogen content, a relationship that holds across species and growth forms (Field and Mooney

1986).

Nutrients are excellent parameters to monitor when assessing the impact of a management activity on ecosystem resistance and resilience, because nitrogen integrates ecosystem function across many different levels (e.g., nitrogen deficiencies create a positive feedback between decreased productivity and slowed decomposition rates). Using indices related to nutrient use and cycling may be especially important at sites where nutrients limit plant growth and influence carbon allocation. (Vogt et al. 1997).

HOW IS NUTRIENT CYCLING AFFECTED BY HUMAN ACTIVITIES?

Human activities, such as land clearing and erosion, can cause the loss of nutrients (e.g., phosphorus), disrupt the natural cycling of nutrients, and limit ecosystem productivity. At the same time, agriculture and industry can discharge excessive amounts of nutrients (e.g., nitrogen) into natural ecosystems, drastically change their trophic structure, and degrade water quality. The extent of damage suffered by natural ecosystems depends on the degree to which nutrient levels deviate from natural levels.

The link between nutrient availability and productivity of agriculture has led to the widespread increase in the use of synthetic fertilizers with many deleterious effects on the environment (Smil 1997). Many past and current land uses also directly altered natural nutrient cycles, typically resulting in an excess input of nutrients from additional applications and greater runoff. Whatever their source, air and water emissions of nitrogen compounds are ultimately deposited as nutrients on terrestrial and aquatic ecosystems.

By overloading the capacity of ecosystems to cycle nitrogen within the natural communities, inputs can seriously contaminate both ground and surface waters with consequent adverse effects on human health. Depending on the hydrologic cycle (many of the same agricultural practices also increase runoff), fertilizer nitrogen can easily travel along watercourses to ponds, lakes, estuaries, or ocean bays resulting in eutrophication. Frequently eutrophied waters suffer algal blooms that reduce oxygen levels when the algae die and decompose, resulting in fish kills and other food chain effects. Long Island Sound in New York and San Francisco Bay in California are currently suffering eutrophication as a result of increased nitrogen loads from a variety of urban and agricultural sources.

Wastewater discharges are another important source of excessive nutrients in aquatic systems. Lake Washington near Seattle was an early example of an important recreational lake where large quantities of nutrients, especially phosphorus, resulted in eutrophication and blooms of the blue-green alga, *Oscillatoria rubescens* (NRC 1992). Public concern and scientific predictions that the natural nutrient cycling and water quality conditions of the lake could be restored led to the diversion of wastewater discharges to Puget Sound. The scientific projections for rapid improvement in lake condition were borne out after the diversion. Nuisance algal blooms were no longer a threat; nitrogen was no longer limiting because of the reduced algal biomass; and lake transparency increased several fold. The much larger volume of Puget Sound enabled its nutrient cycling to withstand the additional inputs.

In contrast, the continual nutrient enrichment of water flowing into the Everglades from agricultural runoff has affected the nutrient cycling in the Everglades and Florida Bay, which is becoming an aquatic dead zone. In the natural Everglades ecosystem, nutrients for plant growth were derived principally from rainfall and were widely distributed and assimilated into the carbonate-based system resulting in low concentrations of nutrients throughout the fresh and saline waters. Nutrient enrichment is changing the Everglades from its natural oligotrophic condition, resulting in the replacement of its unique flora with exotic plants that can out compete the natives when nutrients are elevated (Harwell 1997).

The persistence of nitrogen-based fertilizers on the land contributes to acidification and the increased loss of trace nutrients and release of heavy metals. Within the soil, bacteria generate nitrous oxide from fertilizers. Although the concentrations of this gas are low, they contribute to the serious problems of ozone destruction in the stratosphere and greenhouse warming in the troposphere. Microbes acting on fertilizer also produce nitric oxides, which react in the presence of sunlight to make photochemical smog. The emissions of nitrogen compounds from combustion can affect ecosystems far removed from the source. The deposition of nitrogen compounds can overload nutrient-sensitive ecosystems such as Chesapeake Bay. The nutrient enrichment problem in Chesapeake Bay includes a 25% atmospheric loading component and has decreased water clarity to the point where bay grasses, which support a wide array of other organisms, have been eliminated from many areas (U.S. EPA 1982).

In addition to the local-scale disturbance of nutrient cycling in ecosystems, alteration in the carbon and nitrogen cycles can drive global changes in the earth's chemistry. Increased fluxes of carbon to the atmosphere that occur when land is converted to agriculture or when wetlands are drained, contribute to the build-up of the greenhouse gases, carbon dioxide and methane, in the atmosphere. Nitrogen-fixation, biomass burning, and tropical land clearing increase nitrogen oxides and affect the stratospheric ozone shield. These and other changes in the nitrogen cycle also cause acidic precipitation and pollution of freshwater, estuarine, and coastal marine ecosystems, resulting in eutrophication and contamination of ground and surface drinking water by high nitrate-nitrogen levels (Daily et al. 1997).

Even relatively small inputs of nutrients (particularly nitrogen and phosphorus) can adversely affect low-fertility ecosystems. When these systems are enriched with nutrients, grasses often dominate, and broadleaf plants decline. In North American old fields, nutrient-enriched sites supported lower species richness and weedy annual, non-native flora rather than the perennial grasses typical of the region (Carson and Barrett 1988). In another example, annual forbs were replaced by non-native grasses in Californian serpentine grassland with predominantly nutrient-poor soils (Huenneke et al. 1990). Hobbs and Atkins (1988) discovered that the combination of nutrient enrichment and physical soil disturbance produced the greatest effect in enhancing the establishment and growth of non-native species.

Artificial depletion of nutrients can also degrade ecosystem functioning and facilitate the invasion of exotic species. Intensive forestry and agricultural harvests can directly remove substantial amounts of nutrients and degrade soil fertility. At the same time, the loss of forest nutrient inputs to streams that result from logging or forest conversion can reduce the productivity of invertebrates and the fish that prey on them. Overgrazing and other activities contributing to soil losses and impoverishment can change the vegetation composition and associated organisms in rangelands.

Lands abandoned from human use generally support early successional vegetation (with higher rates of nutrient absorption and photosynthesis), which can also result in the depletion of internal nutrient reserves and greater incidence of disease (Chapin 1983). The different nutrient cycling characteristics of exotic plants that successfully invade these disturbed habitats may drastically alter nutrient cycling, e.g., exotic actinorrhizal nitrogen-fixers in nitrogen-deficient regions can change nitrogen budgets and successional processes of native vegetation (Vitousek 1990).

HOW CAN ADVERSE EFFECTS ON NUTRIENT CYCLING BE MITIGATED?

In mitigating adverse effects on nutrient cycling in ecosystems, as with other ecological processes, the manager needs to take his cue from nature. Ascertaining the appropriate levels and timing of nutrient inputs and outputs, using historical information or reference ecosystems, should be the basis for modifying project activities. In some cases, the mitigation goal will be to remove excessive nutrient inputs (or remove nutrients by treatment or biomass harvesting), while in others the mitigation goal will be to replace nutrients lost because of the project.

At the same time, these simple mitigation goals should be placed in the context of the whole ecosystem. In naturally low-fertility ecosystems degraded by nutrient enrichment, managers may use the cropping and removal of plant biomass to achieve proper phosphorus levels. Obviously such mitigation procedures need to consider the role of plants as habitat and components of other ecological processes. Other options include grazing, burning, or mowing to decrease the likelihood of nutrient accumulations (Green 1972). Simple fixes, such as applying fertilizer to replace lost nutrients, will likely miss other components needed to maintain a balanced mineral nutrition for the resident organisms (Vogt et al. 1997). As yet, the interactions between mineral nutrition and other factors such as disease and pests, carbon allocation, and defense mechanisms are poorly understood; nonetheless, these interactions may be critical in determining our capacity to successfully manage natural ecosystems. For example, the manager should not automatically seek to eliminate early successional species in hopes of increasing production. Such pioneering species might be important for nitrogen fixing, serving as hosts to mycorrhizae that are needed by later succession species, pumping essential elements to the conifer rooting zone from below, or restoring channels in the soil.

As described above, inputs of excessive amount of nutrients into aquatic ecosystems is the most common deleterious effect on nutrient cycling. Reduction of excessive nutrient loading to sensitive ecosystems can by reduced by (NRC 1992)

- diverting point sources of nutrients or nutrient-laden streams out of a watershed
- modifying products to contain lower amounts of nutrients
- removing nutrients from wastewater in engineered treatment systems
- intercepting nutrients in pre-lake impoundments (e.g., storm water retention ponds or wetlands)
- decreasing nutrient runoff from agricultural lands by BMPs

- instituting land use and management controls on development
- controlling air emissions of nitrogen oxides

While diversion of nutrient inputs out of the source watershed is usually too difficult or costly, diversions away from sensitive lakes into manmade impoundments or into irrigation systems for agriculture (and golf courses) are increasing. The other growing practice is to intercept nutrients from nonpoint sources by "soft" technologies such as retention ponds, wetlands, and sediment fencing. Artificial wetlands are an especially promising method as they are generally effective in retaining both suspended solids and metals such as lead and zinc, as well as phosphorus (Martin 1988). Diversion to natural wetlands is less effective and may result in additional adverse effects (Richardson 1988).

Links between nutrient cycling and other ecological processes. The nutrient cycling of an ecosystem is closely linked to other processes discussed in this document. The presence of critical habitats (EP-1), such as wetlands, and their distribution in the landscape (EP-2), strongly influence the transport of nutrients, usually in conjunction with hydrological patterns (EP-5). Structural diversity (EP-4) in the form of dead wood and leaf litter contribute to terrestrial and aquatic nutrient pools. Natural disturbances (EP-3) disrupt nutrient flow and can facilitate the invasion of exotic species with consequences for biotic interactions (EP-8) and population dynamics (EP-9). When the natural capacity to cycle nutrients is degraded, pollutants accumulate, and ecosystems no longer purify waste inputs (EP-7).

REFERENCES

Carson, W.P. and G.W. Barrett. 1988. Succession in old-field plant communities: Effects of contrasting types of nutrient enrichment. *Ecology* 69:984-994.

Chapin, F.S. 1983. Patterns of nutrient absorption and use by plant form natural and man-modified environments. In Mooney, H.A. and M. Godron, eds. *Disturbance and Ecosystem: Components of Response*. Springer-Verlag, Berlin.

Daily, G.C., P.A. Matson, and P.M. Vitousek. 1997. Ecosystem services supplied by soil. In G.C. Daily, ed. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC.

Field, C. And H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. In Givnish, T.J., ed. *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge, MA.

Green, B.H. 1972. The relevance of seral eutrophication and plant competition to the management of successional communities. *Biological Conservation* 4:378-384.

Harwell, M.A. 1997. Ecosystem management of south Florida. *BioScience 47:499-512.*

Hobbs, R.J. and L.F. Huenneke. 1988. Disturbance, diversity, and invasion: Implication for conservation. *Conservation Biology* 6:324-337.

Huenneke, L.F., S.P. Hamburg, R. Koide, H.A. Mooney, and P.M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71:478-491.

Krebs, C.J. 1978. *Ecology: The Experimental Analysis of Distribution and Abundance.* Second Edition. Harper & Row, Publishers, New York.

Lassoie, J.P. and T.M. Hinckley. 1991. *Techniques and Approaches in Forest Tree Ecophysiology.* CRC Press, FL.

Martin, E.H. 1988. Effectiveness of an urban runoff detention pond-wetlands system. *American Society of Civil Engineers, Journal of Environmental Engineering Division* 114:810-827.

National Research Council. 1992. *Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy*. National Academy Press. Washington, D.C. 552 pp.

Noss, Reed F., and Allen Y. Cooperrider. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press.

Odum, E.P. 1971. *Fundamentals of Ecology*. Third edition. Saunders, Philadelphia, PA.

Richardson, C.J. 1988. Freshwater wetlands: Transformers, filters, or sinks? *Forem* (Duke University, Durham, NC) 11:3-9.

Smil, V. 1997. Global population and the nitrogen cycle. *Scientific American* July 1997:76-81.

Swank, W.T. 1988. Stream chemistry responses to disturbances. In Swank, W.T., and D.A. Crossley, Jr., eds. Forest Hydrology and Ecology at Coweeta. Ecological Studies. Vol. 66. Springer-Verlag, New York.

U.S. EPA. 1982. Chesapeake Bay Program Technical Studies: A Synthesis. Chesapeake Bay Program, Annapolis, MD.

Vitousek, P.M. 1990. Biological invasions and ecological processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7-13.

Vogt, K.A., J.C. Gordon, J.P. Wargo, D.J. Vogt, H. Asbjornsen, P.A. Palmiotto, H.J. Clark, J.L. O'Hara, W.S. Keaton, T. Patel-Weynand, and E. Witten. 1997. *Ecosystems: Balancing Science with Management*. Springer, New York.

7. PURIFICATION SERVICES

DEFINITION

Ecosystems naturally purify the air and water. They also detoxify and decompose both natural and manmade wastes. Purification processes are necessary for the normal functioning of ecosystems; they break down harmful concentrations of toxic materials and refertilize soils and sediments through the action of microbes and other organisms. The capacity of ecosystems to assimilate and recycle waste material depends on physical, chemical, and biological mechanisms; this capacity may be exceeded by anthropogenic inputs depending on system-specific conditions.

WHAT CONSTITUTES PURIFICATION SERVICES AND HOW DO THEY CONTRIBUTE TO ECOLOGICAL INTEGRITY?

In 1864, George Perkins Marsh wrote

"The carnivorous, and often the herbivorous insects render an important service to man by consuming and decaying animal and vegetable matter, the decomposition of which would otherwise fill the air with effluvia noxious to health."

The natural process of decomposition is critical to ecosystem health and the recycling of nutrients and energy that sustains life. As with the other processes that characterize ecosystems, the ability to assimilate wastes and provide clean air, water, and soil has evolved to suit the conditions of the environment over time. Natural systems have finite capacities for assimilating wastes and detoxifying contaminants; certain compounds (especially those created by artificial processes) are highly resistant to decomposition and amenable to bioconcentration in animal tissues. Excessive inputs of wastes, the removal of critical species, or the alteration of other ecological processes (e.g., hydrology) can disrupt the purification process and degrade the ecosystem.

Purification services rid the environment of dead organic matter and waste associated with the production and consumption of food, fodder, timber, cotton and other fiber, biomass fuels, and pharmaceuticals. This ability is taxed when humans use the land, streams and rivers, estuaries, oceans, and atmosphere to dispose of unwanted material. Inorganic nutrients (nitrogen and phosphorus) are discharged into waters from sewage wastewater and are deposited from the air as nitrogenous compounds originally emitted into the atmosphere by the burning of fossil fuels. Organic wastes from sewage, animal processing, and agricultural lands may contain bacterial pollutants as well as nutrients.

Aquatic ecosystems act upon these materials in a variety of ways to transform them, detoxify them, or sequester them. Aquatic systems process nutrients by the uptake of plants, especially phytoplankton but also riparian wetland vegetation. Each aquatic ecosystem has a finite capacity to degrade the organic matter produced by natural and anthropogenic activities. Excessive eutrophication reduces ecosystem services through anoxia and nuisance algal blooms. Hypereutrophication transforms the entire aquatic ecosystem into one that can no longer oxidize organic wastes (Elmgren 1989).

In estuaries, bivalve molluscs act as filters, potentially removing excess algal production and forestalling the effects of eutrophication. Newell (1988) calculated that at historic levels of natural abundance, the oysters of Chesapeake Bay filtered a volume equal to the bay every three days. Filter feeding by benthic animals is an important purification service that may compensate for excess additions of nutrients.

Wetlands are among the most effective ecosystems for removing pollutants and purifying wastes. Wetlands process pollutants and wastes by (1) incorporation into or attachment to wetland sediments or biota, (2) degradation, or (3) export to the atmosphere or groundwater (Strecker et al. 1992). Wetlands operate through a series of interdependent physical, chemical, and biological mechanisms that include sedimentation, adsorption, precipitation and dissolution, filtration, biochemical interactions, volatilization and aerosol formation, and infiltration. Because of the large variation in the hydrology, sediments, biota, and other characteristics of wetlands, means that the dominant mechanism of pollutant removal and efficiency varies from wetland to wetland.

Sedimentation is a solid-liquid separation process in which gravitational settling removes suspended solids; it is primarily responsible for removing pollutants from the water column (Strecker et al. 1992). Hydrology plays a critical role in favoring sedimentation over floatation in wetlands. Adsorption onto the surfaces of suspended particulates, sediments, vegetation, and organic matter is the principal mechanism for removal of dissolved pollutants. Adsorption increases the longer the water is in contact with underlying soils and organic matter. Many ionic pollutants (e.g., metals) dissolve or precipitate in response to changes in the solution chemistry of wetlands. Filtration is the simple sieve-like removal of pollutants and sediments from the water column by vegetation.

Wetland plants and other vegetative systems can increase the assimilation of pollutants into the system through interactions with the soil, water, and air (Chan et al. 1982). Plants provide surfaces for bacterial growth and adsorption, filtration, nutrient assimilation, and the uptake of heavy metals. In an aerobic environment, nitrifying bacteria convert ammonia ions into nitrate for uptake by plants, and in an anaerobic environment, nitrate is converted to nitrogen gas (denitrification) (Reddy et al. 1982). The rate of these processes increases with increasing temperature and microbial activity.

Soil microbes also consume wastes and the remains of dead plants and animals, rendering their potential toxins and human pathogens harmless, while recycling their constituent materials into forms usable by plants.

HOW SHOULD PURIFICATION SERVICES BE DESCRIBED?

The level of purification services provided by ecosystems has been approximated by comparison to equivalent waste assimilation and detoxification activities of human-constructed treatment facilities. Primary treatment (removal of solids by sedimentation, flocculation, screening, or similar methods), secondary treatment (removal of organic matter and nutrients by biological decomposition using methods such as aeration, trickling filters, or activated sludge), and tertiary treatment (removal of 50% to 90% of nutrient and dissolved solids using a variety of methods) generally produce water of a particular quality and have associated costs (Cutter et al. 1991). The marginal value of using aquatic ecosystems to scrub nutrients from sewage wastewater can be estimated by using standard engineering formulae to calculate the costs of construction and operation of each of these treatment technologies (Peterson and Lubchenco 1997).

The specific quality of the water (usually the absence of non-natural substances in non-natural quantities) can be measured against state-designated water quality standards (required under the federal Clean Water Act). The analyst can evaluate whether the ecosystem is providing purification services by considering the amount of contaminants above standard thresholds. Purification services are degraded when the loading of nutrients or other wastes exceeds the capacity to transform these wastes microbially. In the case of synthetic compounds (i.e, those not found in nature), the capacity for assimilation or degradation by natural ecosystems may be very limited. General categories of substances that may exceed natural levels in ecosystems where purification services have been degraded include (Cutter et al. 1991)

- disease-causing organisms (bacteria, viruses, and parasites)

- particulate organic matter (a burden to assimilation capacity of ecosystems usually described as total suspended solids or biochemical oxygen demand)
- particulate and dissolved inorganic solids (another component of total suspended solids that is generally inert but influences the deposition of trace substances)
- nutrients (primarily nitrogen and phosphorus as triggers to algal blooms)
- heat (from industrial discharges and lack of stream shading)
- synthetic organics (pesticides and industrial organics such as PCBs that may bioaccumulate or bioconcentrate in the food chain)
- metals (arsenic, lead, mercury, and many others that are toxic in low concentrations but only available to organisms under certain circumstances)
- radioactivity

Many techniques have been developed to measure the presence, concentrations (in air, water, soil, and tissues), and dissipation rates of these diverse groups of substances. As discussed in Section 6--Nutrient Cycling, the effectiveness of natural ecological processes for handling nutrients can be measured by changes in the trophic status of the water body. If a naturally oligotrophic lake becomes eutrophic, it indicates that the nutrient cycling has changed and that the purification services are no longer effective. In the case of petroleum hydrocarbons, naturally occurring microbes can detoxify these compounds and ultimately degrade them into carbon dioxide and water (Cerniglia and Heitcamp 1989). This valuable purification service may cease if anoxia eliminates the necessary aerobic conditions. The most toxic substances produced by industrial processes (e.g., DDT, PCBs, dioxins) are not so readily degraded and transformed by natural ecological processes. Ecosystems can sometimes sequester these compounds in river, lake, or ocean sediments, rending them generally unavailable to organisms. Although not strictly a purification process, the decrease in available contaminant concentrations is a measure of ecological service provided to the ecosystem and humans.

HOW ARE PURIFICATION SERVICES AFFECTED BY HUMAN ACTIVITIES?

The discharge of contaminants to the air, land, and water (resulting from industrial processes, municipal wastewater, automobile traffic, and many other human activities) often overwhelm the purification capabilities of natural ecosystems. Recognition of this problem was the impetus for the Clear Air Act, Clean Water Act, and many other environmental statutes. These laws provide remedies for the excessive introduction of nutrients and toxic substances into the environment. To assess environmental impacts, the analyst needs to determine when changes in community composition and ecological processes (e.g., hydrology and nutrient cycling) will compromise the ability of the ecosystem to purify wastes and sustain the natural condition.

When purification services fail, hot spots of toxic contamination can kill or injure plants and animals. Certain toxic chemicals can accumulate or concentrate in organisms as they are taken up and passed on through the food chain. There are many examples of contaminants reaching levels where the purification processes are modified or overwhelmed. In aquatic systems where the buffering capacity of the surrounding soils is low, acidic deposition from atmospheric emissions results in acidification of lakes and streams with toxic effects on fish and other organisms. Fish are now absent from many otherwise pristine lakes in the Adirondacks and Canada. Ozone and other air pollutants can adversely affect forest and agricultural ecosystems. Periodic industrial discharges of toxic chemicals can eliminate sensitive aquatic organisms, producing subtle changes in aquatic communities. Fat-soluble contaminants such as PCBs can bioconcentrate in predatory mammals and birds, reaching highly toxic levels or impairing reproduction (Cutter et al. 1991).

Petroleum hydrocarbons are routinely released and spilled into the environment. When in association with sediment particles, petroleum hydrocarbons are deposited on the floors of estuaries and oceans, where naturally occurring microbes detoxify these compounds and ultimately degrade them into carbon dioxide and water (Cerniglia and Heitcamp 1989). Because this process is aerobic, nutrient induced anoxia can eliminate this valuable detoxification service. To some degree, estuarine and marine ecosystems can transform heavy metals by binding them with sediments such that they become biologically unavailable (Peterson and Lubchenco 1997). These and other pollutants (such as DDT, PCBs and dioxins), however, often are not transformed into harmless compounds and instead present biological hazards (Long and Morgan 1990). In some cases, organically mediated sedimentation onto the sea floor helps bury and isolate much of this waste, but at other times complete isolation and sequestration of these materials does not occur (Peterson and Lubchenco 1997).

The ability of ecosystems to effectively transform, degrade, or sequester these wastes depends on the kind of contaminant involved and the purification mechanism of the specific ecosystem. Few studies have focused specifically on changes that reduce an ecosystem's ability to purify wastes; however, many scientists believe that mismanagement of the American oyster in Chesapeake Bay and other major estuaries in the northeast and mid-Atlantic United States has lead to a decline of almost two orders of magnitude in oyster abundance, reducing the filtering capacity in the Bay from a 3-day cycle to a 3-year cycle, diminishing this important purification process in these waters (Peterson and Lubchenco 1997).

HOW CAN ADVERSE EFFECTS ON PURIFICATION SERVICES BE MITIGATED?

Ecosystems will be most able to continue purifying wastes if they are not overtaxed by additional anthropogenic inputs. Pollution prevention measures and waste treatment alternatives are the best solutions to this problem. Where the composition or structure of an ecosystem has been altered to reduce purification capabilities, restoration of species or processes may be able to mitigate these losses. For example, restoring oysters and other suspension-feeding bivalves may enhance the purification services in estuaries (Carpenter et al 1995).

The history of environmental protection has focused largely on pollution control and clean up. Massive expenditures on research, monitoring, and remediation have occurred since the passage of the Clear Air Act, Clean Water Act, Superfund, and other pollution-oriented laws. Although originally concerned with human health issues, risk assessment science has developed numerous guidelines on what levels of contaminants need to be addressed. The emerging field of ecological risk assessment (Suter 1993) is developing approaches for determining when these contaminants pose hazards to ecological processes as well as species (EPA 1992a). The primary mitigation approach for the analyst should be adherence to defined pollution prevention or clean up goals with more comprehensive consideration of indirect ecosystem effects. Nutrient loading is a good example of where national or even regional standards may not adequately protect the ecosystem-specific ecological processes that provide purification services.

EPA and other agencies have embraced a watershed approach to pollution control that is critical to maintaining the natural purification services of ecosystems (EPA 1992b). Rather than simply cleaning up individual sites, a watershed approach addressed the capacity of the entire system to assimilate and detoxify wastes. To implement this approach, EPA and states are beginning to apply the Total Maximum Daily Load (TMDL) approach to a larger number of pollutants and environmental stressors (EPA 1991).

Wetlands offer special opportunities for mitigating adverse effects on purification services by either (1) protecting the natural water quality improvement processes of wetlands, (2) restoring or enhancing degraded processes, or (3) creating new processes. Although natural wetlands may be able to provide additional nutrient filtering without suffering adverse effects, the creation of new wetlands for the treatment of excessive nutrient loading is preferred (Ewel 1997). In any case, purification services of wetlands can be maintained by ensuring the following conditions:

- adequate flow into wetlands that is slow enough to drop sediments
- a variety of anaerobic and aerobic processes to precipitate or volatilize chemicals from the water column
- accumulation of peat as a permanent sink for many chemicals
- high rates of productivity and mineral uptake leading to accumulation in plant material and burial in sediments
- shallow water and emergent vegetation for significant sediment-plant-water exchange

Links between purification services and other ecological processes. Purification services are closely linked to the other ecological processes discussed in this document. Purification services are fundamentally the result of effective nutrient cycling (EP-6); when the organisms or other factors such as hydrology (EP-5) that govern nutrient processing are degraded, the ability to purify wastes is impaired. Some critical habitats (EP-1), such as wetlands and forests, can effectively process wastes in the water that flow through them. Structural diversity (EP-4) in the form of dense vegetation can sometimes be an effective physical filtering mechanism for wastes. As with other ecological processes, natural disturbance (EP-3) can disrupt the processing of wastes and provide pulses of unassimilated material. Ultimately, effective processing and assimilation of potentially toxic material benefits the population dynamics (EP-9) of native species; where natives suffer from toxic contamination, exotic species may invade and degrade biotic interactions (EP-8).

REFERENCES

Carpenter, S.R., S.W. Chisholm, C.J. Krebs, D.W. Schindler, and R.F. Wright. 1995. Ecosystem experiments. *Science* 283:641-683.

Cerniglia, C.E. and M.A. Heitcamp. 1989. Microbial degradation of PAH in the aquatic environment. In U. Varanasi, ed. *Metabolism of Polycyclic Aromatic Hydrocarbons in the Aquatic Environment.* CRC Press, Boca Raton, FL.

Chan, E., T.A. Bunsztynsky, N. Hantzsche, and Y.J. Litwin. 1982. The Use of Wetlands for Water Pollution Control. Municipal Environmental Research Laboratory. U.S. EPA, Cincinnati, OH. EPA-600/S2-82-086.

Cutter, S.L., H.L. Renwick, and W.H. Renwick. 1991. Exploitation, Conservation, Preservation: A Geographical Perspective on Natural Resource Use. Second edition. John Wiley & Sons, New York.

Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea: Energy flows today and at the turn of the century.

Environmental Protection Agency (EPA). 1991. Guidance for Water Quality-Based Decisions: The TMDL Process. Assessment and Watershed Protection Division, U.S. EPA, Washington, DC.

Environmental Protection Agency (EPA). 1992a. Framework for Ecological Risk Assessment. Risk Assessment Forum, U.S. EPA, Washington, DC. EPA/630/R-92/001.

Environmental Protection Agency (EPA). 1992b. The Watershed Protection Approach: An Overview. Office of Water, U.S. EPA, Washington, DC EPA503-9-92-002

Ewel, K.C. 1997. Water quality improvement by wetlands. In G.C. Daily, ed. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC. pp. 329-344.

Long, E.R. and L.G. Morgan. 1990. The Potential for Biological Effects of Sediment-Sorbed Contaminants Tested in the National Status and Trends Program. National Oceanographic and Atmospheric Administration Technical Memo NOS OMA 52. NCAA, Seattle, WA

Marsh, G.P. 1864. *Man and Nature: Physical Geography as Modified by Human Action.*

Scribner. New York.

Newell, R.I.E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? In *Understanding the Estuary: Advances in Chesapeake Bay Research*. Chesapeake Bay Research Consortium, Baltimore, MD. Pp. 536-566.

Peterson, C., and J. Lubchenco. 1997. Marine ecosystem services. In G.C. Daily, ed. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC. pp. 177-194.

Reddy, K.R., P.D. Sacco, D.A. Graetz, K.L. Cambell, and L.R. Sinclair. 1982. Water treatment by aquatic ecosystem: Nutrient removal by reservoirs and flooded fields. *Environmental Management* 6:261-271.

Strecker, E.W., J. M. Kersnar, E.D. Driscoll, and R.R. Horner. 1992. The Use of Wetlands for Controlling Stormwater Pollution. The Terrene Institute, Washington, DC.

Suter, G.W. II. 1993. *Ecological Risk Assessment*. Lewis Publishers, Boca Raton, FL.

8. BIOTIC INTERACTIONS

DEFINITION

The antagonistic and symbiotic interactions among organisms are some of the most important, but least understood, factors influencing the structure of natural ecosystems. Because these interactions have evolved over long periods of time, the deletion of species from or the addition of species to an ecosystem can dramatically alter its composition, structure, and function. Biotic interactions that are particularly important in maintaining community structure or ecosystem function are described as "keystone" interactions.

WHAT CONSTITUTES BIOTIC INTERACTIONS AND HOW DO THEY CONTRIBUTE TO ECOLOGICAL INTEGRITY?

Interactions between organisms are a major determinant of the distribution and abundance of species. They include intraspecific and interspecific competition for resources, predation, parasitism, and mutualism. The outcomes of such direct interactions, however, do not tell the whole story of biotic interactions and their effect on ecosystems. Pimm (1991) argues that unexpected changes in community dynamics are a result of pervasive indirect effects throughout the ecosystem. Disturbances such as the exploitation of a commercially valuable species, a disease outbreak, or the introduction of an exotic species often permeate past the direct effects on "target" species to its competitors, predators, parasites, and beyond (Ostfeld et al. 1996). The far-reaching effects of a disturbance depend on the nature and strength of the target species' connections to other species in the ecosystem. These indirect effects may include feedback loops that propagate or dampen the effect of the original disturbance.

Darwin (1859) described the cascade of biotic interactions by observing that "the number of bumblebees in any district depends in a great measure upon the number of fieldmice, which destroy their combs and nests...the number of mice is largely dependent, as everyone knows, on the number of cats...it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in the district!"

The complexity of biotic interactions is further illustrated by the oak forests of eastern North America. In a model developed by Ostfeld et al. (1996), oak trees (genus *Quercus*) are mast seeders supporting weevils, birds, and mammals, including white-footed mouse, eastern chipmunk, and white-tailed deer. All three mammals are hosts for deer ticks and thus play crucial roles in Lyme disease. Mice are also important predators on gypsy moth pupae and nonoak seeds when acorns are not abundant. Chipmunks are known to be important predators on eggs and nestlings of ground-nesting birds. Chipmunks and mice may be a limiting food resource for predator birds such as barred owls and may compete with seed-eating birds for nonmast seeds. Browsing by deer strongly inhibits growth and survival of understory tree seedlings, which in turn can reduce the abundance and species richness of songbirds. Songbird abundance is also reduced when gypsy moth defoliation increases the vulnerability of nests to predators. Humans are affected by these forest interactions as victims of Lyme disease, as hunters of deer, and as loggers of oak trees. Evidence to date demonstrates that mouse and moth dynamics are relatively short-lived and produce changes in population density over several orders of magnitude, while tree dynamics operate over longer time scales involving much more gradual changes in abundance.

Every ecosystem has a similar story to tell. The interaction between ungulate browsers and vegetation can tip the balance from woodland to savanna; nitrogen-fixing mycorrhizae hasten succession; and size-dependent interactions between predatory fish and herbivorous prey fish may determine the structure of aquatic vegetation communities. The number and relative importance of critical biotic interactions varies with the ecosystem, but in general effects on ecosystem processes are greatest not with changes in a few species but when life-form composition changes (Ewel 1996).

Strong biotic interactions are most common in the cases of predation on competitive dominants, mutualism of pollinators and mycorrhizal fungi, seed dispersal, herbivory that changes vegetative conditions for other grazers, and decomposition of dead matter. Specific examples include

- predation by starfish and sea otter on invertebrates
- production of mast crops
- habitat creation by beaver and gopher tortoise

- nutrient cycling by mycorrhizal fungi and earthworms

The importance of plant-pollinator mutualisms is evident from Burd's (1994) survey of field pollination experiments that concludes that the reproductive success of nearly half of the world's plants may be more limited by pollinator scarcity than by the vagaries of weather, soil fertility, or floral browsers and seed parasites. Strong biotic interactions can also result from predation, competition, diseases, and hybridization with nonindigenous (exotic) species such as kudzu, water hyacinth, purple loosestrife, Japanese beetles, Dutch elm disease, European starlings, common carp, zebra mussels, and melaleuca trees.

The lesson from ecology is that it is important to consider all biotic interactions, because the ecosystem-specific conditions that may change dramatically are most important. Nonetheless, the search for keystone interactions that exert disproportionately large influences on ecological processes is an important and increasingly studied endeavor.

Keystone Interactions. Although the natural function of ecosystems comprises all biotic interactions, the relative importance of these interactions varies: relatively few have a disproportionate role on the structure of the community. The magnitude of the interaction between species is termed the "interaction strength," and species whose effect on their communities is disproportionately large (relative to their abundance) have a high "community importance" and are commonly known as "keystone" species.

Robert Paine (1969) first coined the term keystone for species whose presence is crucial to maintaining the organization of their communities and who are exceptional in their importance. Shortly thereafter, Robert MacArthur (1972) advocated the close scrutiny of interaction strengths among species to further explain the effects of species on their communities. More recently, Power et al. (1996) have developed a more operational definition of keystone species based on the strength of their effect on an ecosystem trait (i.e., community importance). The concept can be extended further to consider "keystone guilds" (as in "diffuse predation" in Menge et al. 1994). The larger system of biotic interactions can be thought of as an "interaction web," analogous to a food web (Carpenter 1988).

By definition keystone species are those that have the strongest interactions; classic examples of keystone species include predatory starfish increasing the diversity of mussel communities by controlling the abundance of dominant prey (Paine 1969), insect pollinators that provide for the reproductive success of at least 67% of flowering plants (Tepedino 1979), beavers that alter the access to resources by modifying their physical environment (Naiman 1988). The ability to identify keystone species based on species traits alone is limited, because keystone species are not necessarily dominant controlling agents in all parts of their range or at all times (i.e., their status as keystones is context dependent). For example, although the original keystone starfish, *Pisaster ochraceus*, is an unambiguous keystone in wave-exposed rocky headlands, in more wave-sheltered habitats, the effect of *Pisaster* predation is weak or nonexistent (Menge et al. 1994).

Ecosystem traits that may be affected by keystone interactions include productivity, nutrient cycling, species richness, or the abundance of one or more functional groups of species. Research indicates that keystone species affecting these traits likely occur in all the world's major ecosystems; that keystone species are not always of high trophic status; and that keystone species can exert effects not only through means other than consumption (Power et al. 1996). Mills et al. (1993) classified these different modes of influence as keystone predators (where increase in the predator extirpates several prey species), keystone prey (where loss of prey may cause predation-sensitive species to disappear and predator populations to crash), keystone mutualists (pollinators or dispersers that support several plant species and their separate food webs), keystone hosts (plants that support generalist pollinators and keystone fruit dispersers), and keystone modifiers or ecosystem engineers (species that mediate other species' access to resources through physical modifications to habitats).

Although keystone species are usually recognized only when direct trophic interactions are involved (Krebs 1985), a broader view of the effect of biotic interactions on ecosystems considers the full range of ecosystem engineering and concludes that keystone engineers occur in virtually all habitats on earth (Jones et al. 1994). Organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials, are called ecosystem engineers (Jones et al. 1994). Although this creation, modification, or maintenance of habitats does not involve direct trophic interaction between species, they are nevertheless important and common. A familiar example is the beaver (*Castor canadensis*) who, by cutting trees and using them to construct dams, influences many ecological processes. Specifically this ecosystem engineer alters hydrology, creating wetlands that may persist for centuries, modify nutrient cycling and decomposition dynamics, retain sediments and organic matter in the channel, modify the structure of the riparian zone, influence the character of water and material transported downstream, and ultimately influence plant and animal community composition and diversity (Naiman 1988)

Keystone engineering effects are often greatest when the resources that are modulated are used by many other species, or when the engineer modulates abiotic forces that affect many other species. Effects on soils, sediments, rocks, hydrology, fire and hurricanes are prime examples. In fact, any effects that extend many lifetimes beyond that of the engineer are likely to have a profound influence (e.g., termite nests, buffalo wallows, beaver dams, and peat).

HOW SHOULD BIOTIC INTERACTIONS BE DESCRIBED?

All species are not created equal in terms of ecosystem structure and function. For instance, most abundant species play a major role in controlling the rates and directions of ecological processes. The dominant species typically provide the major energy and nutrient cycling and the physical structure that supports other organisms (Power et al. 1996). More surprisingly, but still well supported in the literature, is the phenomena of less abundant species with much larger effects on their ecosystems than would be predicted from their abundance.

The environmental analyst must identify interactions among species and the relative strengths of these interactions. Network or system diagrams are a valuable tool for developing the conceptual models of ecosystem interactions (CEQ 1997). Such diagrams relate the component species, guilds, or trophic levels in a chain or web of causality and allow the user to trace cause and effect through a series of potential links. They allow the user to analyze the multiple, subsidiary effects of projects on biotic interactions.

Community ecology is an entire scientific discipline devoted to studying the interactions among species. This field of basic research explores the possible organization and workings of plant and animal communities as determined by competition, predation, parasitism, or mutualism (Strong et al. 1984). In particular, community ecology can provide analysts with information about the existence, importance, looseness, transience, and contingency of biotic interactions in different ecosystems. In looking for the influence of biotic interactions on other ecological processes and ultimately ecological integrity, analysts should determine which interactions are intense, persistent, and cybernetic (i.e., operating like an internally controlled system). In simplest terms, this means looking for specific keystone, or otherwise important, interactions.

By definition, removing keystone species causes massive changes in species composition and other ecosystem attributes. For example, removing top predators has a cascading effect throughout the food web, altering species composition and hence physical structure and nutrient cycling (Carpenter et al. 1987). By definition the loss of pollinators and other mutualists will adversely affect their partners, often at the population or species level. Likewise, the removal of keystone engineers can eliminate habitat modifications that support entire communities. A primary aspect of measuring biotic interactions for environmental analysis is to identify keystone predators, mutualists, engineers, and other species that operate in the ecosystem of concern.

In the case of keystone ecosystem engineers, six factors should be evaluated to determine their likely influence on the ecosystem (Jones et al. 1994):

- lifetime per capita activity of individual organisms
- population density
- the spatial distribution of the population, both locally and regionally
- the length of time the population has been present at the site
- the durability of constructs, artifacts, and impacts in the absence of the original engineer

- the number and types of source flows that are modulated by the constructs and artifacts, and the number of other species dependent upon these flows

Gophers are examples of keystone engineers living at high densities, over large areas for a long time, giving rise to structures (mima mounds) that persist for millennia and which affect many resource flows.

The potential for invasion by exotic species is another important aspect of identifying and quantifying biotic interactions that may affect the ecosystem. Because exotic species come from different environmental settings, they are not generally as well adapted as native species (although in degraded ecosystems they may be better adapted). When conditions are favorable, however, they can be very successful (lacking the constraints of co-evolved predators and competitors) and dramatically change the biotic interactions in the ecosystem. The presence of or potential invasion by nonindigenous (exotic) species such as kudzu, water hyacinth, purple loosestrife, Japanese beetles, Dutch elm disease, European starlings, common carp, zebra mussels, and melaleuca trees has profound implications for biotic interactions.

HOW ARE BIOTIC INTERACTIONS AFFECTED BY HUMAN ACTIVITIES?

Human activities affect individual species (and through biotic interactions many other species and ecological processes) by direct exploitation, habitat elimination, and modification of ecological processes. By changing the access of species to their food, shelter, and reproduction, human activities initiate a cascade of biotic interactions that can affect entire ecosystems. In fact, the elimination of biotic interactions may be more difficult to notice than the extinction of individual species, because one of the partners may persist after the other is gone because of long-lived individuals or compensation mechanisms (Janzen 1974).

The destruction or degradation of habitats involves the loss and modification of vegetation. This has obvious implications for plant-animal and animal-animal interactions. Holling (1992) points out that forests "make their own weather and the animals living therein are exposed to more moderate and slower variation in temperature and moisture than they would otherwise be." In this general way, habitat loss affects biotic interactions. When the effects eliminate or reduce keystone species, more specific interactions are affected.

The elimination (or drastic reduction) of keystone species from over-exploitation, animal control activities, or habitat destruction can cause population explosions of species no longer controlled, or the loss of species dependent on the keystone species. In a well-known example, the over-hunting of sea otters off the Pacific Coast of the United States released the keystone predation by sea otters on sea urchins, a grazer on kelp. When the populations of sea urchins were unchecked, they eliminated the kelp beds, in turn changing wave action and siltation rates, and profoundly affecting other inshore flora and fauna (Estes and Palmisano 1974). The effects on the keystone predator (sea otter) effects were perpetuated through the ecosystem by effects on two ecosystem engineers (sea urchin and kelp). Over-hunting directly on the American alligator (another ecosystem engineer) had a similar effect, reducing the number of alligator wallows, a habitat used by many species in the southeastern United States. The burrows of the protected gopher tortoise continue to be damaged by land conversion and recreational and military activities, eliminating habitat for 400 other species, including those that live only in these burrows (obligate commensals).

In addition to keystone predators and ecosystem engineers, keystone mutualists such as pollinators, are being adversely affected by human activities. Pollinators are threatened by habitat alteration, introductions of alien pollinators, and pesticide poisoning (Bond 1994). In North America, honeybee numbers have declined 25% since 1990, and natural pollination systems have been disrupted in many parts of the world (Kearns and Inouye 1997). Agriculture, grazing, fragmentation of native landscapes, and development of areas that once supported wild vegetation all cause the loss of native food plants, rendezvous plants, and nesting sites used by pollinators. Modifications of water supplies can affect pollination because both ground- and cavity-nesting bees require shallow water edges to collect water for nest construction. Habitat fragmentation can reduce flower population size below the threshold of some density-dependent foraging pollinators (the Allee effects; Lamont et al. 1993). Broad-spectrum insecticides such as those used to control grasshoppers on rangelands in the southwestern United States kill many more insects than grasshoppers, including pollinators. The mid-April to late May grasshopper spraying campaigns overlap the flowering period of many endemic rangeland plants and the period of emergence and active foraging of most native bee species (Kearns and Inouye 1997).

Disruption of plant-pollinator mutualisms can create a cascade of events affecting multiple species. In tropical communities, fig trees are keystone species. Each of the approximately 800 fig tree species depends on a unique tiny wasp for pollination. If the population of fig trees drops below 300, the wasp population may not be sustained, and the food base for primates, procyonids, marsupials, toucans, and other birds species could collapse (LaSalle and Gauld 1993).

The effect of disrupting pollination depends on whether the plant-pollinator mutualism is facultative or obligate, and the importance of seed production in the demography of the plant. The plants most at risk from loss of a pollinator are those that are either dioecious (with different male and female plants) or self-incompatible (requiring pollen from other plants), those that have a single pollinator, and those that propagate only by seeds. The large number of honeybees in some habitats can result in intense competition with many different native flower visitors.

Invasion of Exotic Species. A successful invasion by exotic species can be devastating for ecosystems. Because the change in ecological dynamics is biological, it is not confined by a finite geographic area or number of organisms. In most cases, it is impossible to eradicate or even effectively limit the numbers of exotic species. Exotic invasions are the most visible and likely most damaging evidence of disrupted biotic interactions.

From an economic perspective, introduced insects that consume crop plants are the most destructive. The Mediterranean fruit fly, boll weevil, corn borer, and other insects have caused billions of dollars of damage despite massive control campaigns (Pfadt 1985). From an ecological perspective, the most destructive exotic herbivores are generalist species introduced to islands, such as goats, pigs, and rabbits. Excessive grazing obviously eliminates or degrades the vegetation upon which many other species depend, creating a cascade of deleterious biotic interactions.

Exotic parasites and pathogens have direct effects on native species, often severely reducing numbers or eradicating populations altogether. The extinction of several Hawaiian birds has been attributed to infections of avian pox and avian malaria made possible by the introduction of the exotic mosquito vector, *Culex quinquefasciatus* (Van Riper et al. 1986). Pathogens can have wide ranging effects on entire ecosystems, as in the chesnut blight that completely restructured North American temperate deciduous forests (Newhouse 1990). Accidental introductions are not the only problem; species introduced as biological control agents should be carefully scrutinized (Howarth 1991). The purposeful introduction of mongoose, supposed predators on the exotic Norway rat, has wreaked havoc in several ecosystems, most notably in Hawaii, where the mongoose preferentially attacks endemic species such as ground nesting birds. The decline in some species of butterflies may be attributable to the more than one hundred species of parasites, pathogens, and predators that have been imported into the United States in an attempt to control gypsy moths (Hunter 1996). The adverse effects of exotics as competitors are most conspicuous with plants and sedentary species, such as kudzu, zebra mussels, purple loosestrife, and water hyacinth (Hunter 1996). Although these species compete primarily for space (and the water, nutrients, and light that come with it), other exotics compete for a single resource. For example the European starling displaces eastern bluebirds from nest cavities in the eastern United States.

The effects of exotics are not restricted to species losses; many ecological processes can be adversely affected. Famous examples include the severe soil erosion on Round Island following overgrazing by rabbits and goats, and the disruption of trophic structure in Lake Victoria with the introduction of the Nile Perch (Hunter 1996). Exotic plants have many ways to drastically alter ecosystem processes including (1) exotic nitrogen-fixing plants altering soil chemistry, (2) fire-prone exotic plants causing fires to burn more extensively, (3) floating aquatic weeds blanketing waterbodies and changing water chemistry, and (4) exotic plants with deep root systems and high rates of transpiration lowering water tables (Vitousek 1986).

HOW CAN ADVERSE EFFECTS ON BIOTIC INTERACTIONS BE MITIGATED?

Successfully mitigating adverse effects on biotic interactions depends on a thorough understanding of these interactions. Three general principles apply to avoiding, reducing, or compensating for effects on biotic interactions:

- Carefully consider the consequences of the loss of species for which no obvious role in the ecosystem has been discovered. Guard against the loss of organisms with disproportionately high community importance values.

- Eradicate introduced alien species that may have strong effects (i.e., may become keystone species with adverse effects on native species) before they become well established.
- Apply an adaptive management approach. The understanding and management of potential keystone species is often limited, and the full ramifications can only be determined by adjusting project implementation according to monitoring results.

The ultimate fate of many plants may depend on preserving their mutualistic relationships with pollinators and with the web of organisms that affect both plant and pollinator. To minimize harm to native pollinators, insecticides should not be applied during a plant's flowering period; however, because many native bees produce multiple broods per summer, after-flowering pesticide applications may still decrease the pollinator population for the subsequent year. Also, land managers should avoid spraying pesticides under climatic conditions that enhance toxicity or on flower or foliage altogether (e.g., on bait for pests such as grasshoppers). Where crops that are not well served by declining honey bees, managers should set aside pesticide-free habitat for potential natural pollinators in nearby wild habitats.

Although management of pollination systems is relatively untried, protecting natural habitat probably will be the most successful approach (e.g., leaving unplowed strips of land between agricultural fields to encourage nesting by native bees). In addition, reducing fragmentation may prevent decreases in pollination and seed production, and protecting a range of plant species may preserve a season-long supply of nectar and pollen. More active measures include controlled burns to control wood plants and maintain communities of herbaceous plants that provide appropriate floral resources for pollinators. Some native pollinators may be reintroduced if populations of competing invaders can be controlled.

Links between biotic interactions and other ecological processes. Biotic interactions are closely linked to the other ecological processes discussed in this document. Critical habitats (EP-1) obviously provide the food and shelter for dependent species and the pattern of patches of these habitats (EP-2) play an important role in mediating interaction between species (such as vulnerability of songbirds to nest predation from cowbirds that penetrate forest edges). The indirect effects of natural and anthropogenic disturbance regimes (EP-3) usually extend through the ecosystem as biotic interactions. Structural complexity (EP-4) in many ecosystems can mediate biotic interactions by providing refuge for prey and partitioning resources. The converse is also true; for example the depression of herbivore prey populations (e.g., sea urchins) by predators (e.g., sea otters) allows the growth of spatially heterogenous kelp communities. Changes in hydrologic patterns (EP-5) or nutrient cycling (EP-6) can also affect biotic interactions, giving competitive advantages to species that are better adapted to the new levels of resources. Biotic interactions of many kinds play critical roles the population dynamics of species (EP-9) and ultimately their genetic diversity (EP-10).

REFERENCES

Bond, W.J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society, London B Biological Sciences* 344:83-90.

Burd, M. 1994. Bateman's principle and plant reproduction: The role of pollen limitation in fruit and seed set. *Botanical Review* 60:81-109.

Carpenter, S.R. 1988. *Complex Interactions in Lake Communities*. Springer, New York.

Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer, X. He, and C.N. von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863-1876.

Council on Environmental Quality (CEQ). 1997. Considering Cumulative Effects Under the National Environmental Policy Act. CEQ, Executive Office of the President, Washington, DC.

Darwin, C.R. 1859. *On the Origin of Species By Means of Natural Selection*. John Murray, London, UK.

Estes, J.A. and J.F. Palmisano. 1974. Sea-otters: Their role in structuring nearshore communities. *Science* 185:1058-1060.

Ewel, J.J. 1996. Ecosystem processes and the new conservation theory. In Pickett, S.T.A., R.S. Ostfeld, M. Shachak, and G.E. Likens, eds. 1996. The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity. Chapman and Hall, New York. pp. 252-261.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447-502.

Howarth, F.G. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36:485-509.

Hunter, M.L., Jr. 1996. *Fundamentals of Conservation Biology*. Blackwell Science, Cambridge, MA.

Janzen, D.H. 1974. The deflowering of Central America. *Natural History* 83:49-53.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.

Kearns, C.A. and D.W. Inouye. 1997. Pollinators, flowering plants, and conservation biology. BioScience 47:297-307.

Krebs, C.J. 1985. *Ecology. The experimental analysis of distribution and abundance.* Third ed. Harper and Row. New York.

Lamont, B.B., P.G.L. Klinkhamer, and E.T.F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in a demonstration of the Allee effect. *Oecologia* 94:446-450.

LaSalle, J. And I.D. Gauld. 1993. Hymenoptera: Their diversity, and their impact on the diversity of other organisms. In J. LaSalle and I.D. Gauld, eds. *Hymenoptera and biodiversity*. C.A.B. International, Oxon, UK. Pp. 1-26.

MacArthur, R. 1972. Strong, or weak, interactions. *Transactions of the Connecticut Academy of Arts and Sciences* 44:177-188.

Menge, G.A., E.L. Berlow, C.A. Blanchette, S.A. Navarrete, and S.B. Yamada. 1994. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249-287.

Mills, L.D., M.E. Soule, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219224.

Naiman, R.J. 1988. Animal influences on ecosystem dynamics. *BioScience* 38:750-752.

Newhouse, J.R. 1990. Chestnut blight. *Scientific American* 263:106-111.

Ostfeld, R.S., C.G. Jones, and J.O. Wolff. 1996. Of mice and mast. *BioScience* 46:323-330.

Paine, R.T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91-93.

Pfadt, R.E. 1985. *Fundamental of Applied Entomology*. 4th edition. Macmilllan Publishing Company, New York.

Pimm, S. L. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities.* University of Chicago, Chicago, IL.

Power, M.E., D. Tilman, J.A. Estes, B.A. Menge, W.J. Bond, L.S. Mills, G. Daily, J.C. Castilla, J. Lubchenco, and R.T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609-620.

Strong, D.R, Jr., D. Simberloff, L.G. Abele, and A.B. Thistle. 1983. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, NJ.

Tepedino, V.J. 1979. The importance of bees and other insect pollinators in maintaining floral species composition. *Great Basin Naturalist* 3:139-151.

Van Riper, C., III, S.G. van Riper, M.L. Goff, and M. Laird. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* 56:327-344.

Vitousek, P.M. 1986. Biological invasions and ecosystem properties: Can species make a difference? In Mooney, H.A. and J.A. Drake, eds. *Ecology of Biological Invasions of North America and Hawaii.* Springer-Verlag, New York. pp. 163-176.

9. POPULATION DYNAMICS

DEFINITION

The population is a critical unit, not only for evolutionary change, but for the functioning of ecosystems. Population numbers alone do not adequately reflect the prospects for species or the continued performance of their ecological role. Information about life history and population dynamics, such as dispersion, fertility, recruitment, and mortality rates, is critical to identifying potential effects on population persistence and ecological processes. Key factor analysis can determine which links in these dynamics primarily affect population success, while population viability analysis can predict the amount and distribution of habitat needed to maintain healthy populations.

WHAT CONSTITUTES POPULATION DYNAMICS AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

When populations are lost, the local adaptations of these populations are lost, the ecosystem functions performed by these populations cease, and ultimately species may go extinct. In general, the risk of losing populations (and with them ecological integrity) is greatest when populations are small, but even large populations may have critical components of their life histories or population cycles that make them especially vulnerable. These critical components include

- age structure and sex ratios

- population regulation, stability, dispersion, and movements
- behavioral habitat selection, mating systems, and social interactions

The genetic makeup of populations is also important (see Section 10--Genetic Diversity). Different species will have different key factors in their population dynamics that are critical to population persistence; when these factors are adversely affected, population numbers decline and ecosystem functions may also decrease. For example, species vary in their patterns of dispersion in space, density, dispersal, and migratory behavior. Migratory birds and fish may have very different stresses or capacities for increase in their breeding and nonbreeding habitats. An environmental insult may have a completely different effect in one habitat than in another. The need to migrate itself may be the weak link for many species, making them susceptible to dams (e.g., anadromous fish) or highways (e.g., vernal pool-breeding amphibians). Populations that congregate in small areas may also be at special risk from adverse effects, as are populations that are effectively isolated from immigration (e.g., geographic or habitat islands).

Small populations. The higher risk of extinction in small populations is a result of stochastic (random), rather than deterministic (cause and effect) processes (Brussard 1991). Predicting species persistence requires understanding the roles of genetic (inbreeding depression and genetic drift) and demographic (random variation in birth and death rates) stochasticity, as well as the far greater roles of environmental stochasticity, including catastrophes (Soule 1987). Demographic stochasticities may include skewed sex ratios (slowing or dooming reproduction) and distorted age structure (either reducing critical parental protection of immature or eliminating fertile age classes). Although genetic and demographic stochasticity usually only affects populations of less than 30 individuals, larger populations that inhabit small areas may be eliminated by unpredictable storms, diseases, or even late freezes.

The importance of population size for the survival of populations and the persistence of their ecological functioning means that analysts need to pay special attention to rare populations. Although rarity is a commonly used term, it includes at least seven different distributional patterns (Rabinowitz et al. 1986). Rarity may result from one or more of the following: highly restricted geographic range, high habitat specificity, or small local population size. Different types of rarity make populations vulnerable to different extinction processes. Highly endemic species may be abundant, but because they occur at few locations, they are at greater risk from stochastic environmental events, as well as intentional habitat destruction. Species with special habitat requirements are vulnerable to actions that affect their habitat everywhere it occurs, such as climate change. Widespread species with low population numbers are vulnerable to the loss of genetic diversity.

Metapopulations. In addition to focusing on small populations, analysts needs to recognize that an apparently large population may actually be a collection of smaller, sink and source subpopulations (i.e., be a "metapopulation"). Subpopulations in high-quality habitats that support local reproductive success greater than local mortality are termed "sources," while subpopulations in low-quality habitats where local reproductive success is less than local mortality are termed "sinks" (Pulliam 1988). Populations are distributed across the environment in habitats of variable quality; each of these subpopulations contributes to the larger metapopulation that ultimately determines species viability. Good quality habitats usually support the source populations with excess reproduction continually colonizing the poorer quality habitats that can only support sink subpopulations. The lesson for ecosystem management is that elimination or degradation of subpopulations will disproportionately affect species survival if these subpopulations are sources (i.e., preservation of sink subpopulations only cannot protect a species). The important implication is that population density may overestimate the resiliency of a population to losses of individuals. A loss of relatively few individuals may devastate the population if the habitat supporting the source subpopulation is eliminated; therefore, it is important to determine not only where the species is most common but where it is most productive.

HOW SHOULD POPULATION DYNAMICS BE DESCRIBED?

Information about the life history and population dynamics of species potentially affected by federal actions can be critical to understanding how populations and their ecological functions will change. However, although populations are influenced by many factors, all are not equally important; often a few dominate the dynamics. Key factor analysis is a method for identifying and understanding the stages of an organism's life history in which critical controlling processes occur. By partitioning the variance in each element of the life table among environmental causes, the key factors that cause high mortality are identified. Species with complex life histories, such as salmon, may have independent controls at different stages because these stages use different resources or live in different habitats.

Key factors may be related to behavior such as inflexible habitat selection, rigid mating systems, or complex social interactions. There may be sensitive stages in demography involving age or size-specific growth rates, age structure, or sex ratios and sex biases. They may involve fragile population stability or easily disrupted dispersion and population movements. Promising studies in comparative plant demography suggest that we may be able to make generalizations about which stages in the life history are critical based on life-history categories. Often these key factors relate to strict habitat requirements. Once these habitats are modified, the population consequences can be severe.

Population Viability Analysis, or PVA, can help analysts better understand population dynamics of species and predict consequences on ecosystems (Gilpin and Soule 1986). PVA evaluates the population, life history, habitat, genetic, and other data needed to predict the likelihood that a given population in a given place will persist for a specific amount of time. Although there are no consistent and accepted methods for its practice, the review by Boyce (1992) describes many excellent studies that have demonstrated the utility of PVA. Using a combination of field observation, field experimentation, and modeling, PVA can combine the vital information on (1) the relevant pattern of rarity, (2) the dynamics of source and sink subpopulations, and (3) inherent life history parameters to define the conditions under which there is a 95% probability that the population will persist for 100 years (or other persistence goal). In its final form, a PVA usually produces a model of habitat type, quality, quantity, and pattern that support the species of concern (Shaffer 1981).

HOW ARE POPULATION DYNAMICS AFFECTED BY HUMAN ACTIVITIES?

Many of the influences of anthropogenic disturbance are first felt on life-history characteristics such as age-specific survivorship, fecundity, and fertility. The decline of species from habitat destruction, over-harvesting, poisoning, or the myriad of indirect and cumulative effects rarely involves proportional losses throughout the population. Depending on which life stages and age classes are most severely affected, species slowly rebuild their populations or quickly collapse. All extinctions ultimately result from changes in demographic traits.

Given their demographic traits, species will respond differently to human intervention, such as fishing pressure. Cod populations can withstand some fishing pressure because individual females grow to a larger size faster when cod density is reduced, thus producing more offspring more quickly (Solbrig 1991). Species with less flexible life histories, such as whales, are at much greater risk of extinction. These differences in demography have important implications for impact analysis (e.g., At what point will fishing pressure reduce the reproductive life span below the interval between good recruitment years and cause the collapse of the fishery?).

There are many examples of populations that have crashed after a critical stage in the life cycle was affected. Fisheries managers have identified many such problems, but managers have frequently failed to institute controls in time. Such crashes in populations can lead to a breakdown of ecological functions and vice versa. In a non-fisheries example, much of the southeastern forest of the United States has been fragmented to the point that the fragments are devoid of the fungal activity needed for denitrification, decomposition, and other functions. The lack of fire in managed forests can prevent recruitment of young trees because their seeds won't germinate unless heated in a fire. In both these forests, the preponderance of adult trees gives the impression of population health, but in reality the age class is skewed, the recruitment is low, and the population is headed for collapse.

Population dynamics play an equally important, but opposite, role in the success of introduced species. Non-native species that have life history and population dynamics that respond favorably to new environments can explode and overwhelm natives whose populations are structured to adapt more slowly. Many of the most dramatic examples of population fluctuations affecting ecological processes involve the invasion of non-native (exotic) species. Through direct biotic interactions (predation and competition) and indirect interactions (ecological engineering and habitat modification), invasive species can disrupt the natural population dynamics of native species. The lessons of small population size and the key factors affecting the persistence of species (i.e., those weak links that cause them to fail) can be marshalled in pest control efforts as we endeavor to reverse native population degradation by eliminating exotic species (Holsinger 1995).

HOW CAN ADVERSE EFFECTS ON POPULATION DYNAMICS BE MITIGATED?

Adverse effects on population dynamics manifest themselves in the loss of species, populations, or genetic diversity (see Section 10--Genetic Diversity). Understanding the population dynamics of affected species is critical to developing interventions to avoid, minimize, or compensate population loss or decline. An entire field of scientific research, population biology, is focused on the variations and adaptations of populations (Dawson and King 1971). The legacy of these observational, experimental, and theoretical efforts has been to produce a good understanding of how populations work. In addition, the applied sciences of fisheries and wildlife management have produced numerous techniques for evaluating the status of populations and designing management actions.

Managing populations means applying the tools of PVA and metapopulation analysis to develop a thorough understanding of their life-stage and life-table characteristics. Once the changes in population dynamics are identified, the wildlife or fisheries manager should draw on available techniques to (1) provide resources that may be scarce, (2) control threats such as predators, especially humans, and (3) directly manipulate populations, such as moving individuals to new sites (Hunter 1996).

Most populations at risk of extirpation are small; therefore, the primary focus in mitigating adverse effects on population dynamics is to avoid affecting the life stages or population behaviors that determine population size. Most often this means maintaining adequate quality habitat and access to it at the appropriate times. When populations have already declined to low levels, managers may need to provide essential resources until the population increases. In environments where degrading stresses may still persist, some success may be obtained by making sure food sources and water are available at least at the most vulnerable life stages.

When subpopulations are extirpated, individuals may need to be moved. Unfortunately, failures are more common than successes. Out of 80 translocation projects for endangered birds and mammals undertaken in Australia, Canada, New Zealand, and the United States, only 44% were successful (Griffith et al. 1989). Among the success stories are the return of several North American game species (e.g., wood duck, desert bighorn sheep, white-tailed deer, wild turkey) to a substantial portion of their original range following near extirpation from overhunting. Even in cases where adequate numbers can be moved and proper husbandry provided, concerns about disease transmission and genetic effects (see Section 10--Genetic Diversity) argue for a cautious approach to species translocation.

Populations at risk of extirpation may also need management to provide access to migration corridors or special habitats for critical life stages. The blockage of migration upstream and downstream by dams can effectively eliminate once huge runs (subpopulations) of anadromous (and to a lesser extent catadromous) fish species. Proper design and implementation of fish ladders and other passage structures are primary means of mitigating these population effects in existing and planned impoundments. Similarly, if populations need to breed during a certain season, conflicting activities should be postponed. If most recruitment is limited to a specific habitat, that habitat should be high priority for preservation.

The lessons of fisheries and wildlife management teach us that exploitation (hunting or other consumptive uses) of wild populations by humans may have small to very large effects on population dynamics and persistence (Hunter 1996). Ideally, human consumption of organisms should be confined to "compensatory mortality" (i.e., harvesting that does not increase the natural mortality rate of a population). When exploitation results in "additive mortality" the overall number of deaths is greater than naturally occurs (from starvation and other factors). After determining the appropriate level of harvest, the wildlife or fisheries manager can use any of the following methods to limit exploitation:

- the number of organisms taken (often protecting a sex or age class that is critical to population dynamics)
- who can harvest
- how they can harvest
- where they can harvest (usually protecting nurseries or other critical areas)
- when they can harvest (usually avoiding nesting seasons and other sensitive periods).

The details of how fish, game, and timber harvests can be managed is reviewed by Smith (1986) and Strickland et al. (1994).

Links between population dynamics and other ecological processes. Population dynamics are closely linked to the other ecological processes discussed in this document. Obviously, population success depends on an abundance of critical habitats (EP-1). At the same time, certain species depend a pattern of habitats (EP-2) that are large (e.g., forest interior-dwelling songbirds) or well-connected (e.g., migratory fish). Natural disturbance regimes (EP-3) often drive population dynamics, including providing for seed germination and other critical life stages. Structural complexity (EP-4) and hydrologic patterns (EP-5) may also provide essential refuges or nesting sites for many critical life stages. Anadromous salmon and other migratory species provide substantial biomass and nitrogen for nutrient cycling (EP-6) in ecosystems. The inherent population dynamics of many species play an important role in natural biotic interactions (EP-8) and are closely tied to genetic diversity (EP-10).

REFERENCES

Boyce, M.S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics*

23:481-506.

Brussard, P. 1991. The role of ecology in biological conservation. *Ecological Applications* 1:6-12.

Dawson, P.S. and C.E. King. 1971. *Readings in Population Biology*. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Gilpin, M.E. and M.E. Soule. 1986. Minimum viable populations: Processes of species extinction. In Soule, M.E., ed. *Conservation Biology*: The Science of Scarcity and Diversity. Sinauer, Sunderland, MA. pp. 19-34.

Griffith, B, J.M. Scott, J.W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool. Status and strategy. *Science* 245:477-480.

Holsinger, K.E. 1995. Population biology for policy makers. BioScience Supplement 1995:S-10 to S-20.

Hunter, M.L., Jr. 1996. *Fundamentals of Conservation Biology*. Blackwell Science, Cambridge, MA.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.

Rabinowitz, D., S. Carins, and T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In M.E. Soule, ed., Conservation Biology: The Science of Scarcity and Diversity, Sinauer Associates, Inc., Sunderland, MA. pp. 182-204.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131-134.

Smith, D.M. 1986. *The Practice of Silviculture*. 8th edition. John Wiley and Sons, New York.

Solbrig, O.T. 1991. From Genes to Ecosystems: A Research Agenda for Biodiversity. Report of a IUBS-SCOPE-UNESCO workshop. The International Union of Biological Sciences, Cambridge, MA.

Soule, M.E. ed. 1987. *Viable Populations for Conservation*. Cambridge University Press, UK.

Strickland, M.D., H.J. Harju, K.R. McCaffery, H.W. Miller, L.M. Smith, and R.J. Stoll. 1994. Harvest management. In Bookhout, T.A., ed. *Research and Management Techniques for*

Wildlife and Habitats. The Wildlife Society, Bethesda, MD.

10. GENETIC DIVERSITY

DEFINITION

Diversity at the genetic level underlies the more visible diversity of life that we see expressed in individuals, populations, and species. Over evolutionary time, the genetic diversity of individuals within and among populations of species contributes to the complex interplay of biological and nonbiological components of ecosystems. The preservation of genetic diversity is critical to maintaining a reservoir of evolutionary potential for adaptation to future stresses.

WHAT CONSTITUTES GENETIC DIVERSITY AND HOW DOES IT CONTRIBUTE TO ECOLOGICAL INTEGRITY?

Genetic diversity originates at the molecular level and is the result of the accumulation of mutations, many of which have been molded by natural selection. The genetic variants found in nature are integrated not only into the physiological and biochemical functions of the organism, but also into the ecological framework of the species. The genetic diversity of a species is a resource that cannot be replaced (Solbrig 1991).

Ecological processes are the product of evolution, and genetic diversity is the basis of the evolutionary process. Genetic diversity enables a population to respond to natural selection, helping it adapt to changes in selective regimes. Evidence from plant and animal breeding indicates that genetic diversity promotes disease resistance. These and other results support the concept that the reduction of genetic diversity may increase the probability of extinction in populations.

While no general principles can be applied, research results from several systems indicate that genetic diversity can both positively and negatively influence population dynamics (Solbrig 1991). It is also possible that genetic variation in birth and death rates may stabilize interactions between competing species. Through its effects on interspecific interactions, genetic diversity could even affect ecosystem dynamics and stability. For example, genetically mixed stands of some crops have shown a higher rate of production than single cultivar stands.

There are three main ways that genetic diversity possessed by a species affects its long-term survival:

- Heterozygosity (multiple alleles at the same gene) is positively related to fitness (i.e., the organism's ability to perform its essential biological functions and reproduce)

- The rate of evolutionary change that can occur in a group of organisms depends on the amount of variation in the gene pool (i.e., the fuel that allows the group to change or evolve in response to changing environmental conditions)
- The global pool of genetic information represents the 'blueprint' for all life (i.e., the alleles that have been developed over time by the process of mutation and are sustained in the populations by natural selection)

Historically, concern over genetic diversity has focused on overcoming the uniformity of genotypes in crop plants (which makes them vulnerable to new environmental stresses, pests, and diseases) by preserving the range of genetic diversity found in wild relatives (Johnson 1995). Endangered species recovery efforts have sought to broaden the genetic base and overcome inbreeding in remaining populations. More recently, conserving genetic diversity has been targeted for its future utility (Ledig 1988) and it contribution to evolutionary potential (Mlot 1989).

HOW SHOULD GENETIC DIVERSITY BE DESCRIBED?

The number and type of genes available in nature is a valuable resource for medical, agricultural, and other applications. The diversity of gene pools is also important to the extent that it influences populations as the units of evolutionary change. Quantifying the loss of genetic diversity is a way of identifying which populations are most at risk. In some cases, this can be done by analyzing the frequency of certain alleles. One allele is inherited from each parent; they can be identical (have the same DNA sequence) or different from each other. In a stable population, the frequency of particular alleles, or allelic variation, will be fairly stable over time. Whether the population is stable can be calculated by determining the Hardy-Weinberg equilibrium. Laboratory techniques can now be used to measure this allelic variation and determine if populations are at risk of extinction.

Classical methods of estimating the genetic diversity or relatedness among groups of plants have relied upon morphological characters. However, these characters can be influenced by environmental factors. Using molecular and biochemical markers to measure genetic diversity avoids many of the complications of environmental effects acting upon characters by looking directly at variation controlled by genes or by looking at the genetic material itself. Molecular markers represent a powerful and potentially rapid method for characterizing genetic diversity. With molecular markers, direct and accurate measurements of many genetic diversity indicators (heterozygosity, effective population size, allele frequency) can be made (International Plant Genetic Resources Institute 1996).

Practically, analysts usually have to infer effects on genetic diversity from data on population numbers and structure. Determining that the population has dropped below a critical minimum size (causing genetic drift) or that important source and sink populations within a metapopulation have been lost can be useful signs that genetic diversity is degrading.

HOW IS GENETIC DIVERSITY AFFECTED BY HUMAN ACTIVITIES?

Biological depletion occurs not only when species are threatened but when their gene pools are reduced through the elimination of their populations (Meffe and Carroll 1994). In addition, genetic diversity is degraded when representatives of certain genotypes (and phenotypes) are eliminated from a population. This can occur through direct harvesting, destruction of habitat, and interactions with exotic species. The introduction of hatchery-raised or domesticated stock is another important situation that may affect the genetic diversity of wild populations.

The "planting" of hatchery-raised fish stock is widespread throughout the United States. The use of nonindigenous species is prevalent, especially in the west where they may make up half of the fish community. Such introduced fish may hybridize with rare local relatives, imperiling the rarer species' genetic integrity (Goodman 1991). In addition, native fish that are stocked may breed with local populations of the same species, disrupting the local stock's ability to adapt to its environment. When hybridization with rare species produces fertile offspring, the genetic identity of the parents can be lost when the offspring of a hybrid backcrosses to the parents. If the stock has been relatively reproductively isolated and adapted to that environment, it may have formed "coadapted gene complexes" that can be disrupted by matings with genetically distinct stocks, leading to introgression that muddies the genetic identity of both stocks. In essence, an incipient species can be driven to extinction through genetic swamping before it has fully arisen (Hunter 1996).

Hybridization between the ubiquitous mallard and the rarer Mexican and Hawaiian ducks is a prime example. Such degradation of the gene pool also has been observed in the Hill Country of Texas with the introduction of smallmouth bass that hybridize with the native Guadalupe. Similarly, many of the more than 10 recognized subspecies of cutthroat trout in western North America are being lost through breeding with introduced rainbow trout.

Less obvious but certainly more widespread factors affecting genetic diversity are habitat destruction and overharvesting. When environmental analysts evaluate a project that causes temporal variation in population size, they should consider whether it could result in a genetic bottleneck and, therefore, a decrease in genetic diversity. Such bottlenecks have been posited as reasons for the poor reproductive success of the Puerto Rican parrot and Florida panther.

Examples of habitat destruction affecting genetic diversity are numerous and often include narrowing the gene pool when satellite populations are lost (e.g., in metapopulations of newts or butterflies). There are also may examples of overharvesting of commercial fish species that have led to the extirpation of important stocks (subpopulations or subspecies). Genetic fitness is also reduced when the most robust individuals in a tree population are selectively harvested as part of forestry management or land development.

HOW CAN ADVERSE EFFECTS ON GENETIC DIVERSITY BE MITIGATED?

The loss of genetic resources following the extinction of species cannot be recovered or mitigated; therefore, the primary task in conserving genetic diversity is to preserve species and protect them from genetic degradation that usually occurs in small populations over time (Meffe and Carroll 1994). This entails maintaining habitat for the critical components of populations dynamics such as life stages, movement, and metapopulation structure (see Section 9--Population Dynamics). Environmental analysts should encourage general habitat preservation and restoration activities, but also focus on habitats supporting populations at the edge of the species ranges that likely have locally adapted gene complexes.

More specific mitigations are available for the conservation of genetic diversity when organisms (native or exotic) are introduced to meet recreational goals or to facilitate recovery of species. One such federal action is the use of hatchery-raised stock for fisheries management. While use of hatchery-raised stock is a possible mitigation, protection of habitat refugia is more important. When hatchery stock are used for planting or species enhancement there is the inherent problem of selecting for domestication and reducing genetic diversity. This can be ameliorated by

- using hatchery stock only as supplementation (i.e., to enhance natural reproduction) and not to replace wild stock
- identifying and using native genetic stocks
- using automatic feeders so fish don't become accustomed to humans and lose their flight response
- not culling for uniform size
- using even sex ratios of spawners (i.e., not fewer males) for the full period of weeks or months that make up the spawning run
- returning to the wild for new brood stock every several generations (Goodman 1991)

The National Fish Broodstock Registry is being developed to provide fisheries personnel with the detailed information on life history, behavior, hatchery, and post-stocking performance needed to effectively manage the resources. This series of databases catalogs information on managed wild and domestic broodstocks of five fish families: trout, catfish, sturgeon and paddlefish, perch, and bass. It consolidates information on origin, breeding practices, reproduction, growth, disease resistance, stress tolerance, post-stocking performance, habitat preference, and genetic characteristics into a standardized data set.

Another kind of federal action is the actual species recovery plan undertaken when species or populations are in decline. The goal of these actions explicitly includes the restoration of genetic diversity because long-term species recovery depends on protecting and managing species genetic resources. Key steps in recovering genetic diversity include

- determining the genetic stocks of the endangered species

- protecting these stocks in refugia
- developing and operating propagation facilities
- planning, implementing, and evaluating augmentation, or reintroduction of genetic stocks in the wild

An approach that can quickly begin preserving the remaining genetic variability is the development of detailed breeding plans specifically designed to preserve the remaining genetic variation. Two examples include (1) the establishment of a specific hatchery broodstock of wild lake trout (Green Lake strain) to assist in recovering this population in Lake Michigan and (2) preservation of a threatened wild white sturgeon population from the Kootenai River, Idaho. In each situation the problem was as follows: (1) the population consisted of a limited number of individuals; (2) the population was expected to be lost or seriously reduced within a short time; and (3) genetic viability would be jeopardized by waiting for long-term habitat restoration programs.

The long-term recovery strategy for fish and other species suffering population declines (and consequent degradation of genetic diversity) involves the following:

- A commitment to use adults captured from the wild broodstock.
- Captured fish are spawned, the offspring are cultured, and the broodstock are returned to the wild.
- Captured males and females are paired to maximize effective population size and equalize the genetic contribution of all individuals to the next generation.
- Culture practices that reduce potential effects of selection are employed.
- Progeny are held in the culture environment until they can survive in the wild.
- During rearing, group identity is maintained so that all pairs contribute equally to the populations stocked.
- The number of fish stocked is the minimum necessary to provide for slow expansion of the wild population and to ensure that stocked fish will not overwhelm the natural wild population.

This approach will begin to restore the natural population structure when successive year classes are produced from the natural population through one entire generation and when low levels of natural reproduction provide year-class cohorts in years when natural reproduction fails to produce successful recruitment. This is especially important to populations that have not had successful recruitment for several years. Two examples of genetic management plans using hatchery operations to restore native stocks are as follows: (1) the Nez Perce Tribe hatchery program (in cooperation with the State of Idaho, the Northwest Power Authority, Bonneville Power Administration and the Fish and Wildlife Service) to protect the genetic diversity of native stocks of chinook salmon and restore them to the Clearwater and (2) development of successful hatchery rearing methods (using DNA analysis and capture information that describes genetic and life history characteristics throughout the range) to address the dramatic declines in lake sturgeon in the Great Lakes and northeastern United States since 1900.

Links between genetic diversity and other ecological processes. Genetic diversity is closely linked to the other ecological processes discussed in this document. It is directly tied to population dynamics (EP-9) and the success of species. Where the abundance (EP-1) or pattern (EP-2) of critical habitats affect population persistence or size, genetic diversity is also affected. Similarly, natural disturbance regimes (EP-3), structural complexity (EP-4), hydrologic patterns (EP-5), nutrient cycling (EP-6), and biotic interactions (EP-8) may strongly affect populations and ultimately genetic diversity.

REFERENCES

Goodman, B. 1991. Keeping anglers happy has a price: Ecological and genetic effects of stocking fish. *BioScience* 41: 294-299.

Hunter, M.L., Jr. 1996. *Fundamentals of Conservation Biology*. Blackwell Science, Cambridge, MA.

International Plant Genetic Resources Institute 1996. Measuring genetic variation. http://www.cgiar.org/IPGRI/training/10-1/5.htm

Johnson, N.C. 1995. Biodiversity in the Balance: Approaches to Setting Geographic Conservation Priorities. World Wildlife Fund, Washington, DC.

Ledig, F.T. 1988. The conservation of diversity in forest trees. *BioScience* 38:471-479.

Meffe, G.K. and C.R. Carroll. 1994. *Principles of Conservation Biology*. Sinauer Associates, Inc., Sunderland, MA.

Mlot, C. 1989. Blueprint for conserving plant diversity. *BioScience* 39:364-368.

Solbrig, O.T. 1991. From Genes to Ecosystems: A Research Agenda for Biodiversity. Report of a IUBS-SCOPE-UNESCO workshop. The International Union of Biological Sciences, Cambridge, MA.