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GAP ANALYSIS: A GEOGRAPHIC APPROACH TO PROTECTION OF BIOLOGICAL DIVERSITY

by

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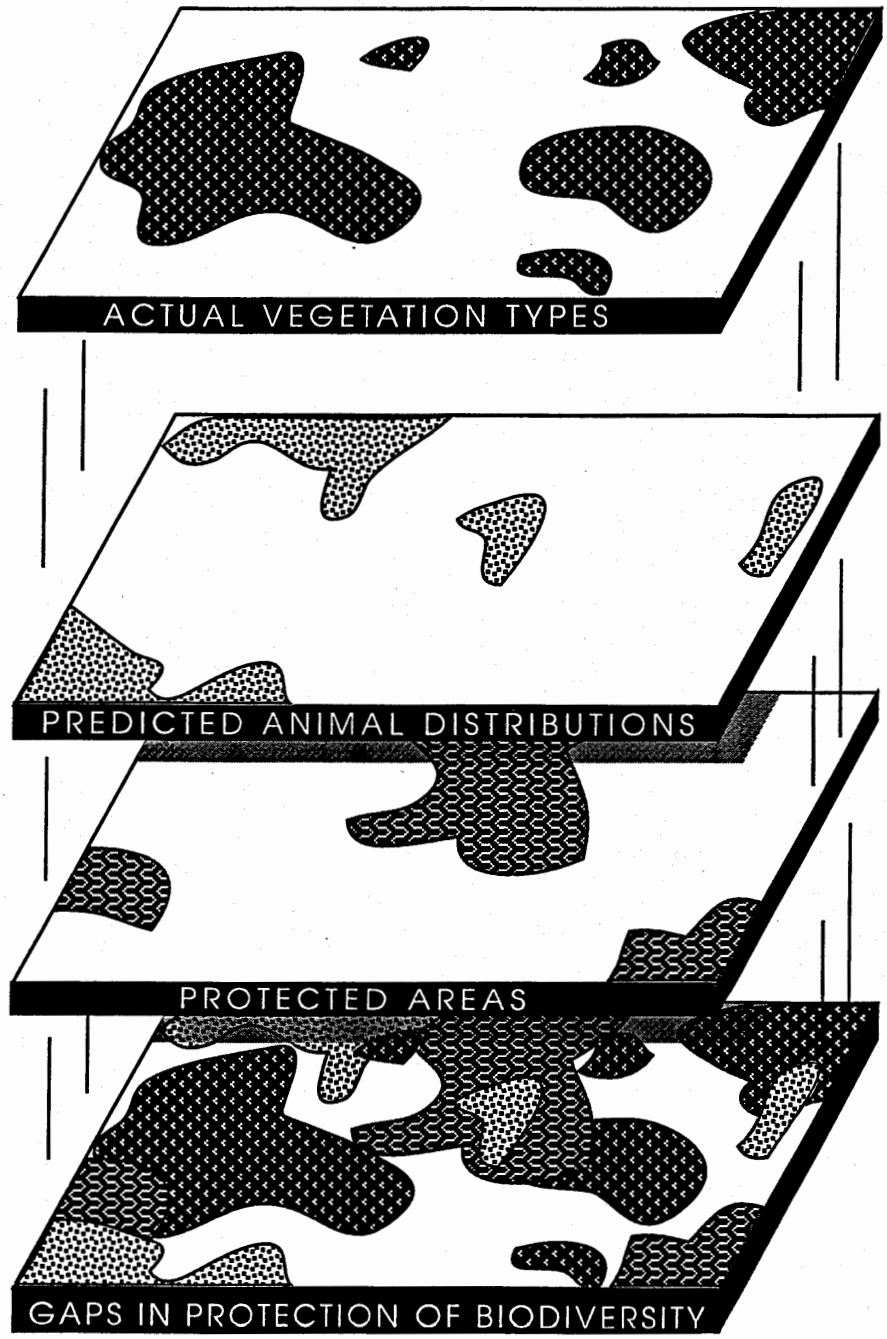
GAP ANALYSIS:

PROTECTING BIODIVERSITY USING GEOGRAPHIC INFORMATION SYSTEMS



FRONTISPIECE. Gap Analysis is the process by which the distribution of species and vegetation types are compared with the distribution of different land management and land ownership classifications. This permits gaps in the protective network for biodiversity to be identified.

GAP ANALYSIS: A GEOGRAPHIC APPROACH TO PROTECTION OF BIOLOGICAL DIVERSITY

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Abstract: The conventional approach to maintaining biological diversity generally has been to proceed species by species and threat by threat. We suggest that piecemeal approaches are not adequate by themselves to address the accelerating extinction crisis and, furthermore, they contribute to an unpredictable ecological and economic environment. Here, we describe a methodology called Gap Analysis, which identifies the gaps in representation of biological diversity (biodiversity) in areas managed exclusively or primarily for the long-term maintenance of populations of native species and natural ecosystems (hereinafter referred to as biodiversity management areas). Once identified, gaps are filled through new reserve acquisitions or designations, or through changes in management practices. The goal is to ensure that all ecosystems and areas rich in species diversity are represented adequately in biodiversity management areas. We believe this proactive strategy will eliminate the need to list many species as threatened or endangered in the future.

Gap Analysis uses vegetation types and vertebrate and butterfly species (and/or other taxa, such as vascular plants, if adequate distributional data are available) as indicators of biodiversity. Maps of existing vegetation are prepared from satellite imagery (LANDSAT) and other sources and entered into a geographic information system (GIS). Because entire states or regions are mapped, the smallest area identified on vegetation maps is 100 ha. Vegetation maps are verified through field checks and examination of aerial photographs.

Predicted species distributions are based on existing range maps and other distributional data, combined with information on the habitat affinities of each species. Distribution maps for individual species are overlaid in the GIS to produce maps of species richness, which can be created for any group of species of biological or political interest. An additional GIS layer of land ownership and management status allows identification of gaps in the representation of vegetation types and centers of species richness in biodiversity management areas through a comparison of the vegetation and species richness maps with ownership and management status maps. Underrepresented plant communities (e.g., present on only 1 or 2 biodiversity management areas or with a small total acreage primarily managed for biodiversity) also can be identified in this manner. Realization of the full potential of Gap Analysis requires regionalization of state data bases and use of the data in resource management and planning.

Gap Analysis is a powerful and efficient first step toward setting land management priorities. It provides focus, direction, and accountability for conservation efforts. Areas identified as important through Gap Analysis can then be examined more closely for their biological qualities and management needs. As a coarse-filter approach to conservation evaluation, Gap Analysis is not a panacea. Limitations related to minimum mapping unit size (where small habitat patches are missed), failure to distinguish among most seral stages, failure to indicate gradual ecotones, and other factors must be recognized so that Gap Analysis can be supplemented by more intensive inventories.

WILDL. MONOGR. 123, 1–41

CONTENTS

INTRODUCTION

The traditional response to the increasing loss of biodiversity has centered on rescuing individual species from the brink of extinction. Typically, high-profile "glamour species" receive most of the attention and funding at the expense of many more species with less public appeal (Pitelka 1981). The reactive, species-by-species approach to conservation has proved difficult, expensive, biased, and inefficient (Hutto et al. 1987; Scott et al. 1987*a*, 1991; Margules 1989; Noss 1991). With limited conservation dollars, recovery of the growing number of listed and candidate endangered and threatened species—now in the thousands in the United States alone—will be exceedingly difficult. The existing system of protected areas managed for their natural values is about 3% of the world's surface area (Reid and Miller 1989) and is about the same percentage for the 48 conterminous United States; this is not sufficient to maintain either species diversity or functional ecosystems (Grumbine 1990).

Biological diversity (biodiversity) is the concept around which new concerns about biological conservation are rallied. Biodiversity refers to the variety and variability among living organisms and the environments in which they occur and is recognized at genetic, species, ecosystem, and often landscape levels of organization (U.S. Congress 1987, Noss 1990). The goal of biodiversity conservation is to reverse the processes of biotic impoverishment at each of these levels of organization. Ecological and evolutionary processes ultimately are as much a concern in a biodiversity conservation strategy as are species diversity and composition. Thus, biodiversity conservation represents a significant step beyond endangered species conservation (Noss 1991, Scott et al. 1991). Most significantly, biodiversity conservation is proactive; it is not confined to last-ditch efforts.

Presuming that a relatively small portion of the total land base will be devoted to biodiversity conservation in the near future, objective techniques are needed to identify and rank proposed conservation areas. Of greatest interest is identification of areas rich in species and vegetation types not already represented in areas managed exclusively or primarily for the long-term maintenance of populations of native species and natural ecosystems (hereinafter referred to as biodiversity management areas). Although a wide variety of conservation evaluation methods have been developed (*see* Usher 1986), only a few have attempted to assess the conservation value of large geographic areas in a quick and

cost-effective manner (e.g., Bolton and Specht 1983, Margules and Austin 1991).

In this monograph, we describe a rapid and efficient method for conservation evaluation of large areas. We call it Gap Analysis, and it is a technically efficient version of the well-established method of identifying gaps in the representation of biodiversity in biodiversity management areas (Scott et al. 1987*a*, 1989, 1991; Burley 1988; Davis et al. 1990). This approach to conservation evaluation has been widely used in Australia (Specht 1975, Bolton and Specht 1983, Pressey and Nicholls 1991), but has seldom been applied to the conterminous United States. Here, we discuss the concept of Gap Analysis; review relevant concepts of vegetation mapping, remote sensing, and geographic information systems (GIS); describe the technique of Gap Analysis; and discuss factors to consider in implementing Gap Analysis for biodiversity conservation.

Acknowledgments.—We thank Malcolm Hunter, James Karr, Roy Kirkpatrick, and John Ratti for constructive criticism of previous drafts of this manuscript. We are indebted to Kathy Merk for preparation of the manuscript. We dedicate this monograph to Prof. Miklos D. F. Udvardy for his contributions to biogeography and biosphere reserve planning.

THE GAP ANALYSIS CONCEPT

Gap Analysis provides a quick overview of the distribution and conservation status of several components of biodiversity. It seeks to identify gaps (i.e., vegetation types and species that are not represented in the network of biodiversity management areas) that may be filled through establishment of new reserves or changes in land management practices. Gap Analysis uses the distribution of actual vegetation types (mapped from satellite imagery) and vertebrate and butterfly species (plus other taxa, if data are available) as indicators of, or surrogates for, biodiversity. Digital map overlays in a GIS are used to identify individual species, species-rich areas, and vegetation types that are unrepresented or underrepresented in existing biodiversity management areas. Not a substitute for a detailed biological inventory, Gap Analysis organizes existing survey information to identify areas of high biodiversity before they are further degraded. It functions as a preliminary step to the more detailed studies needed to establish actual boundaries for potential biodiversity management areas. We hypothesize that Gap Analysis, by focusing on higher levels of biological organization, will be both cheaper and more likely to succeed than conservation programs focused on single species or populations.

Biodiversity inventories can be visualized as "filters" designed to capture elements of biodiversity at various levels of organization. The filter concept has been applied by The Nature Conservancy, which has established "natural heritage programs" in all 50 states, most of which are now operated by state government agencies. The Nature Conservancy employs a fine filter of rare species inventory and protection and a coarse filter of community inventory and protection (Jenkins 1985, Noss 1987*a*). It is estimated that 85–90% of species can be protected by the coarse filter, without having to inventory or plan reserves for those species individually.

The intuitively appealing idea of conserving most biodiversity by maintaining examples of all natural community types has never been tested empirically. Furthermore, the spatial scale at which organisms use the environment differs tremendously among species and depends on body size, food habits, mobility, and other factors (McNab 1963, Harris 1984). Hence, no coarse filter will be a complete assessment of biodiversity protection status and needs. However, species that fall through the pores of the coarse filter, such as narrow endemics and wide-ranging mammals, can be captured by the safety net of the fine filter. Community-level (coarse filter) protection is a complement to, not a substitute for, protection of individual rare species.

Gap Analysis is essentially an expanded

coarse-filter approach to biodiversity protection. The vegetation types mapped in Gap Analysis serve directly as a coarse filter, the goal being to assure adequate representation of all types in biodiversity management areas. Landscapes with great vegetational diversity often are those with high edaphic variety or topographic relief. When elevational diversity is very great, a nearly complete spectrum of vegetation types known from a biological region may occur within a relatively small area. Such areas provide habitat for many species, including those that depend on multiple habitat types to meet life history needs (Diamond 1986, Noss 1987*a*). By using landscape-sized samples (many kilometers across) (Forman and Godron 1986) as an expanded coarse filter, Gap Analysis searches biological regions for areas rich in landscape diversity.

A second filter is based on identifying areas of high species richness (areas of maximum overlap in the ranges of mapped species) and centers of endemism. Although most species will be represented in a set of areas of high species richness, some otherwise widely distributed species, such as large carnivores, may require individual attention. Species with very local or restricted distributions may not occur in areas of high species richness and also may require individual protection. Additional data layers can be used for a more holistic conservation evaluation. These include indicators of stress or risk (human population growth, road density, rate of habitat fragmentation, distribution of pollutants, etc.) and the locations of habitat corridors between wildlands that allow for natural movements of wide-ranging animals and migration of species in response to climate change.

The indicator concept assumes that the attributes being measured (generally, in this case, vegetation, vertebrate, and butterfly distributions) correspond to the broader "endpoint" of concern (overall biodiversity) (Noss 1990). Vegetation is one of the most widely used indirect indicators of the distribution of terrestrial plant and animal species (Austin 1991). Although a number of microhabitat features and other abiotic and biotic factors determine the ultimate suitability of a site for a species, the composition and structure of the dominant vegetation is an important and easily described measure of habitat, especially for animals. A problem with using vegetation as a coarse filter in long range planning, however, is that plant communities break up and assemble in new combinations as species respond individually to climate change (Hunter et al. 1988, Hunter 1991), and vegetation is usually defined by the distribution of dominant species, most of which are habitat generalists.

The major role of vertebrates in community interactions (Terborgh 1988) implies a high correlation between vertebrate species richness and overall biodiversity. This hypothesis cannot be tested empirically until complete species lists (including soil invertebrates, fungi, and microbes) are available from a range of sites. Murphy and Wilcox (1986) suggested that vertebrates often provide a protective umbrella for invertebrate species. However, areas of low vertebrate species richness may contain assemblages of invertebrates, plants, and other organisms of special interest that must be assessed independently.

Butterflies, whose distribution is well documented in many regions, also have been recommended as indicators of overall biodiversity. Pyle (1982) noted several advantages of butterflies as indicators, including moderate vagility, host specificity, an ability to resist the impact of human activities through a high reproductive potential, and species richness high enough to be useful quantitatively yet low enough to be handled efficiently. Butterflies tend to condense the vast amount of ecological information available in plants. Although plant species may be an even better surrogate for overall biodiversity and provide a good supplement to vertebrate- and vegetation-based inventories, detailed plant species distributional data are not available for most western states where the first Gap Analyses are being conducted.

Crumpacker et al. (1988) conducted a Gap Analysis of Potential Natural Vege-

tation (Küchler 1964) in the conterminous United States. They assumed that Federal ownership equaled land protection, an assumption that we believe must be qualified (Scott et al. 1989). However, even with this optimistic assumption, they found that one-fourth of the Potential Natural Vegetation types in the United States were inadequately represented on Federal or Indian lands. To the extent that Potential Natural Vegetation types reflect the current vegetation in an area, they are valuable indicators of biodiversity. However, many areas have been more or less permanently converted to human uses (urban and agricultural areas) or subjected to management practices that alter plant community structure and composition (forests and range lands). In such areas, animals respond to actual vegetation, not potential natural vegetation.

Prior to Gap Analysis, as described in this paper, there was no broad-scale assessment of the protection given actual vegetation types or areas of high species richness in the United States. A Gap Analysis conducted in Hawaii focused on endangered birds (Scott et al. 1986). The distribution of each endangered forest bird species was first plotted individually, based on extensive field inventories. Individual range maps were then combined to obtain a map of species richness for this important group. When compared with a map of the existing reserves, <10% of the ranges of endangered forest birds were protected (Fig. 1). Several of the areas of high endangered bird species richness have since been protected by The Nature Conservancy and state and Federal agencies (Scott et al. 1987*b*).

Gap Analysis products include maps and tables summarizing the predicted distribution and conservation status of vegetation types and species. They also include a conservation evaluation identifying areas potentially rich in vegetation types and species unrepresented or underrepresented in biodiversity management areas. Representation of threatened, endangered, and other species of concern in biodiversity management areas also is evaluated. These products can be used to develop an integrated biodiversity conservation strategy (Scott et al. 1991). Assuming that it is in society's best interest to maintain biodiversity and avoid endangering ever more species, Gap Analysis products can be used to predict the contribution of new biodiversity management areas to the goal of maintaining biodiversity. Field verification of Gap Analysis maps and recommendations at specific sites (at a scale more detailed than that used to verify regional Gap Analysis) is essential prior to any conservation or biodiversity management action.

Given this introduction of the basic concept, how might one embark on a Gap Analysis project? The data layers and sequence of steps in a Gap Analysis (Fig. 2) are ordered logically for efficient execution, but could be rearranged to some degree. Generally, the steps flow through a sequence of mapping, digitizing, and ground-truthing vegetation and species distribution data (Steps 1–4); digitizing biodiversity management area and land ownership maps (5–6); adding point and/or line data for rare species and high-interest habitats, such as wetlands and streams (7); mapping, delineating, and ranking areas of high community diversity and species richness (8–11); identifying the gaps in the protection of vegetation types and species-rich areas (12); and applying these findings to reserve selection and design, land management policy, and other conservation actions (13–15).

VEGETATION MAPPING

Vegetation reflects many physical factors found at a site, such as climate, soil type, elevation, and aspect. It also is composed of the ecosystem's primary producers and it serves as habitat for the animal community. Vegetation acts as an integrator of many of the physical and biological attributes of an area, and a vegetation map can be used as a surrogate for ecosystems in conservation evaluations (Specht 1975, Austin 1991). A vegetation map, therefore,

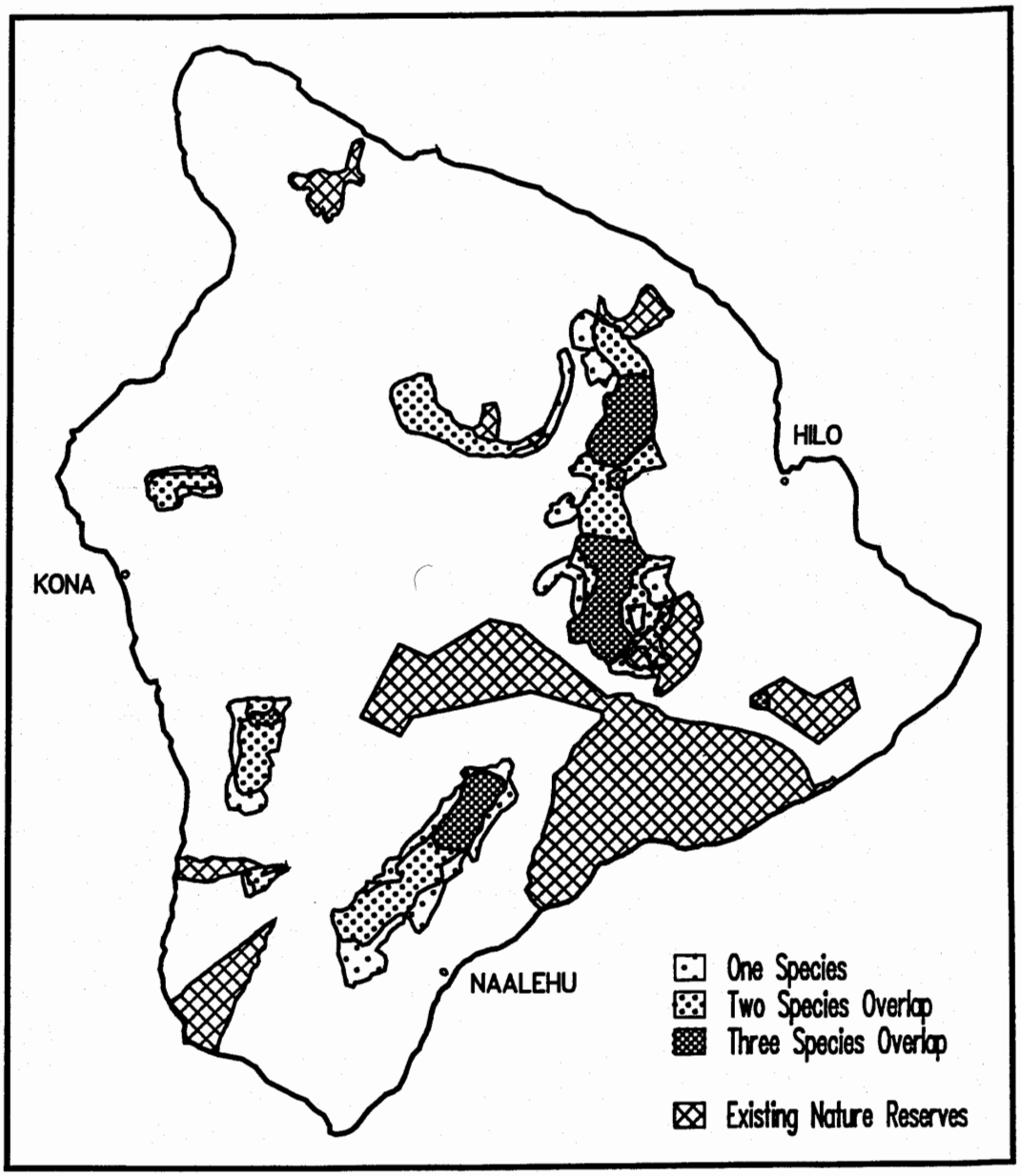

Fig. 1. Distribution of endangered Hawaiian finches in relation to existing nature reserves on the island of Hawaii in 1982 (adapted from Kepler and Scott 1985). The areas of highest species richness for these endangered birds were not protected. Since these data have become available, the 6,693-ha (17,000-acre) Hakalau Forest National Wildlife Refuge has been established in one of the areas of highest species richness. Additional refuges and preserve areas for endangered Hawaiian bird and other species are planned.

provides the foundation for our assessment of the distribution of biodiversity.

This section summarizes the general principles of vegetation classification and mapping and discusses several methods for mapping vegetation patterns. These methods include (1) combining existing vegetation maps for state-wide or regional coverage, (2) visual photointerpretation of satellite photographic images, and (3) dig-

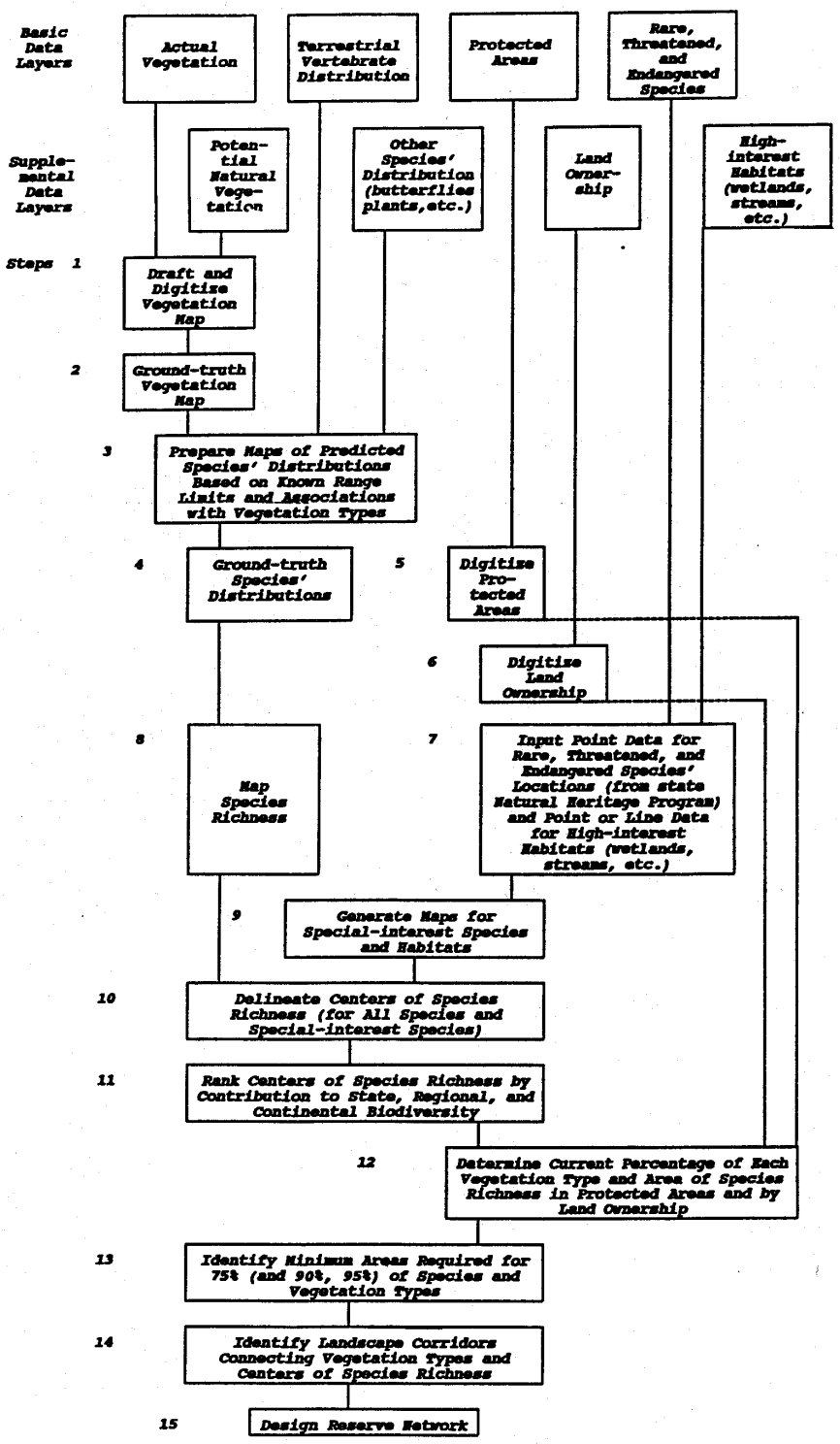

Fig. 2. A flow diagram of the data layers and steps for Gap Analysis.

ital classification of satellite data. A recent review by Küchler and Zonneveld (1988) contains a more comprehensive discussion of the theory and practice of vegetation mapping.

A pilot Gap Analysis program was started in Idaho in 1987 and used a mosaic of existing vegetation maps for this data layer (Method 1). This mosaic was refined by comparison with satellite imagery to identify recent land-use changes. Based on this experience, the second Gap Analysis program started in Oregon in 1989 and relied on prints of satellite imagery to locate the boundaries of vegetation types (Method 2). Third-generation programs (e.g., Utah, California, and Arizona) use a combination of digital image processing, visual photointerpretation of satellite images, and reference to existing vegetation maps and aerial photography to prepare the vegetation data layer. This hybrid approach, which is the standard for future programs, draws on the strengths of all 3 methods, and facilitates consistency in boundary location that is needed for edge-matching maps at state lines.

Vegetation Classification

Several vegetation classification systems are used in the United States and reflect a wide range of user needs and applications. For the purposes of Gap Analysis, classification systems used in vegetation mapping must share the following properties:

1. Vegetation classes must be discriminable in remotely sensed imagery and identifiable in large- to medium-scale aerial photographs.
2. Vegetation classes must correspond to or at least be compatible with recognized vertebrate habitat classification systems.
3. Vegetation classes must describe seral as well as climax vegetation.
4. Vegetation classes used in Gap Analysis by adjacent states should be compatible to allow for regional and national analyses.

Vegetation classifications address scale-dependent spatial and temporal dynamics of vegetation in various ways. Hierarchical classifications have been developed in an attempt to match taxonomic levels with different scales of ecological processes and associated spatial patterns (Küchler and Zonneveld 1988). Some classification systems explicitly recognize seral stages of vegetation, whereas others are based on later seral or climax vegetation. The habitat-typing system of Daubenmire (1952) has been widely used to classify vegetation associations in the western United States. This system is based on the sociofloristic approach developed over the last 80 years and used worldwide (Flahault and Schroter 1910; Braun-Blanquet 1932, 1964; Daubenmire 1952, 1968, 1970; Daubenmire and Daubenmire 1968; Pfister and Arno 1980). The habitat-typing system is based on potential vegetation and assumes that climax plant communities are related to gradients of simple, measurable factors. Indicator species are used to identify habitat types. Because the goal of Gap Analysis is to assess the current status of biodiversity (Scott et al. 1989), indicator species are used to name actual vegetation, usually at the series (*sensu* Driscoll et al. 1984) level. A national hierarchical classification describing these vegetation cover types, compatible at the series level with existing regional and national classifications (e.g., Brown et al. 1980), is being developed in cooperation with The Nature Conservancy (P. S. Bourgeron, The Nature Conservancy, Boulder, Colo., pers. commun.). This classification will allow a standardized name to be used for vegetation types in adjacent states. This standard list of vegetation types is especially important for reconciling independently-developed state vegetation classifications.

Vegetation Mapping Applications for Gap Analysis

No single method of mapping vegetation is best, because the methodology is largely determined by the purposes for which the map will be used (Küchler 1988). A vegetation map prepared for Gap Anal-

ysis of biodiversity serves 2 major purposes. First, it allows quantification of the extent, distribution, and representation in biodiversity management areas of the major vegetation types in a study area. Second, it allows inappropriate habitat to be excluded from predicted distribution maps for individual animal species.

Further uses of the vegetation map may include analysis of the degree and pattern of habitat fragmentation, the location of present or potential linkages between biodiversity management areas, and the identification of landscape-level processes affecting the vegetation (such as fire regimes). The map also is a model of the recent vegetation of a study area, from which predictions can be made about the probable pathways of past and future vegetation change. The map can be updated to quantify changes in vegetation structure and composition resulting from management activities or natural events (e.g., fires, floods, succession). To serve these functions, the vegetation map must contain information on floristic composition and vegetation structure.

Geographic Information System Data Structure

Geographic information systems are computing systems for the storage, display, and analysis of spatial data. Gap Analysis uses GIS because it can perform complicated overlays and spatial analyses that would be difficult and time consuming using traditional cartographic methods. One common use of GIS is the storage of thematic data layers such as vegetation or soil type maps, which can be superimposed on other data layers for analysis.

Data structure refers to the form in which data with known geographic locations are represented and stored in a computer. Data are most commonly represented in a GIS in either raster or vector form (Fig. 3). Satellite measurements are acquired in raster format, whereas much existing GIS software and many widely available data bases are in vector format.

Raster data structure divides space into fields and assigns each field a unique value. The most common structure is the square lattice or grid, a network of uniformly spaced horizontal and perpendicular lines for locating points by means of coordinates. This structure is convenient for imaging systems such as digital satellite remote sensors, which measure radiation reflected or emitted from the earth's surface in a regular array of picture elements (called pixels).

Vector data structure represents spatial information with lines in continuous coordinate space. Lines in the original analog map are stored as strings of coordinates, and the spatial relationships among map entities are stored explicitly or computed when needed. The string of coordinates is closed when the last coordinate point is joined to the first, creating a polygon that approaches the curvature of the analog original. These points, lines, and polygons are the basic unit for data storage and analysis in a vector data structure, and they can have any type of textual information stored about them in an accompanying data base. The evolution of vector-based GIS systems has been driven largely by the desire to encode and analyze existing mapped information. The vector model permits the closest digital approximation to the original map and also retains implicit spatial relationships such as network linkages, object areas, perimeters, and shared boundaries.

Raster and vector data structures each have case-dependent technical and analytical advantages (Burrough 1986). For Gap Analysis, the vector structure is preferred for representing boundaries (e.g., political, land ownership, ecoregions), for storing point observations (e.g., species sighting data, locations of threatened and endangered populations), for representing networks (e.g., roads, streams, habitat corridors), and for mapping generalized land-use or habitat entities (e.g., agricultural regions, ecosystem mosaics, drainage basins). The raster structure is preferred for storing both unclassified and classified imagery, digital elevation data, and other dense maps or continuous surfaces. Con-

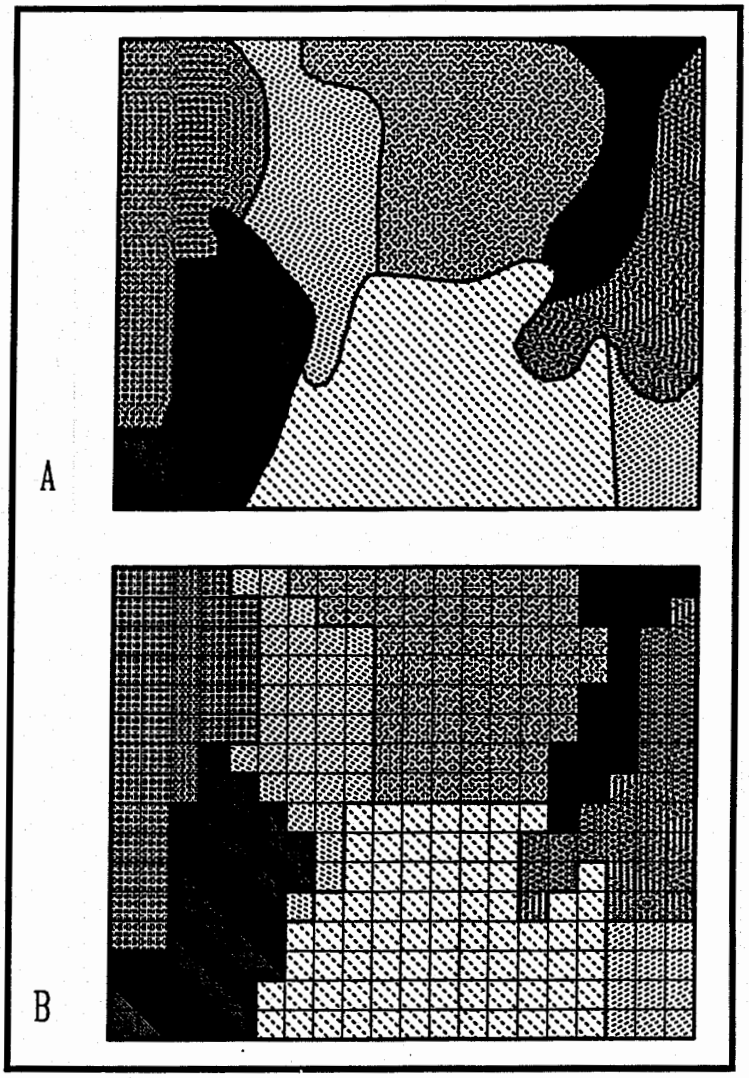

Fig. 3. A heterogeneous area as modeled in a vector-type GIS (A). Same area as modeled by a raster-type GIS (B). Patterns represent areas with different land-cover types.

version of large digital satellite images to vector format is not practical without classifying and greatly simplifying the imagery.

Map Scale, Minimum Mapping Unit, and Image Resolution

Map scale is the ratio of map distance to distance in the real world. For example, on a 1:100,000-scale map, distances are 100,000 times shorter than they are in the real landscape; on a 1:1,000-scale map, distances are only 1,000 times shorter than in the real landscape. The 1:1,000 map is a larger scale because landscape features are represented 100 times larger than they are on the 1:100,000 map. Minimum mapping unit (MMU) refers to the size of the smallest area depicted on a map. Vegetation pattern is highly scale dependent and may vary considerably with map scale and

MMU. Also, the MMU may vary across a map with the taxonomic detail of the vegetation classification system and differing levels of cartographic generalization among map classes and terrain conditions.

Image resolution is used to describe the area covered by pixels in raster maps and may or may not correspond to the scale of the original measurements. For vector maps, resolution refers to the precision of the spatial coordinate system. This depends on digitizing hardware and software and data storage precision and usually is much finer than the precision of the data.

Compiling Existing Vegetation Data for State-wide Mapping

Several potential sources of spatial data should be investigated during the planning stages of a vegetation mapping project. These include remote-sensing data and map data usually available from offices of various Federal, state, and local government agencies. Briefly, the U.S. Department of Agriculture Forest Service's Timber Survey maps, produced through aerial photointerpretation, may be one of the best sources of data on forest vegetation for areas relatively unaltered by timber harvest, fire, or disease. The availability of Bureau of Land Management (BLM) maps varies greatly from state to state. The most useful maps from the U.S. Fish and Wildlife Service (USFWS) are in the National Wetland Inventory map series. Soil Conservation Service soil type maps may be helpful in areas where vegetation data are lacking. United States Geological Survey (USGS) Land-Use and Land-Cover maps are particularly useful, as are the U.S. Environmental Protection Agency's (EPA) ecoregion maps. Maps from state and local agencies often are helpful, but vary widely in quality. Finally, state natural heritage programs are excellent sources on the vegetation of their states. Their scientists and research libraries specialize in information relevant to vegetation mapping, and they may supply valuable leads to obscure vegetation maps and descriptions.

Satellite Remote Sensing of Vegetation

Most states do not have recent vegetation maps with complete and consistent descriptions of actual vegetation types. Satellite imagery is a cost-effective means of producing such maps. For an introduction to the principles and theory of remote sensing, the reader is referred to *The Manual of Remote Sensing* (Colwell 1983) and to recent texts by Richards (1986) and Elachi (1987). Discussion below is limited to sources of up-to-date satellite imagery suitable for regional land-use and land-cover mapping, specifically LANDSAT Thematic Mapper (TM) and Multispectral Scanner (MSS) and Systeme Probatoire d'Observation de la Terre (SPOT) imagery. Loveland et al. (1991) used Advanced Very High Resolution Radiometer (AVHRR) satellite data to produce a national map of land-cover characteristics. This imagery is very useful for frequent monitoring of vegetation characteristics such as greenness, but the large contribution of nonvegetative surface characteristics to the spectral signature of pixels 1 to 4 km on a side make this imagery less useful for mapping the floristic composition and structure of vegetation at the series level.

Basic features of these operational and planned satellite-borne sensors vary in detail and content of what is recorded (Table 1). Recent LANDSAT MSS and TM data have already been collected for most of the United States and are available from the Earth Observation Satellite Company (EOSAT) in a variety of formats. In the context of Gap Analysis, TM imagery has several important advantages over MSS imagery, specifically (1) higher signal-to-noise ratio, (2) higher precision of radiometric data, (3) higher cartographic accuracy, and (4) higher spectral dimensionality (particularly midinfrared bands).

Although the higher spatial resolution of TM data may be important in mapping some features such as wetlands or urban areas, it can actually produce lower clas-

Table 1. Characteristics of operational sensors currently used to map regional land use and vegetation cover.

Satellite series	Sensor	Date available	No. of bands	Spectral sampling[a]	Resolution	Sampling frequency
LANDSAT	MSS	1972	4	VIS/NIR	80 m	16 days
	TM4, 5	1982	7	VIS/NIR/TIR	30/30/120 m	16 days
	TM6	1992	8	VIS/NIR/TIR	20/30/120 m	16 days
NOAA	AVHRR	1978	5	VIS/NIR/TIR	1–4 km	12 hours
SPOT	HRV-P	1986	1	VIS	10 m	3 days
	HRV-XS	1986	3	VIS/NIR	20 m	3 days

[a] VIS = visible light; NIR = near infrared; TIR = thermal infrared.

sification accuracies for many vegetation types that are spectrally heterogeneous at this sampling resolution (open woodlands and shrub lands are especially problematic). A significant drawback to using TM is the high cost relative to MSS. For imagery <2 years old, TM scenes cost 4 times as much as MSS scenes, and MSS imagery >2 years old is very inexpensive. Furthermore, the higher resolution of TM data imposes a 7-fold increase in data volume per band. The advantages cited above, however, make TM data superior to MSS data for digital or manual land-use and land-cover mapping.

The French-owned SPOT remote sensing satellite has been operating since 1986, and data acquisition can be ordered for any location in the continental United States. The SPOT sensor has several assets that make it attractive for biodiversity analysis, including (1) contemporary acquisition, (2) high cartographic quality, (3) high radiometric resolution, (4) late-morning acquisition (reduces shadowing), and (5) multiple viewing angles for better temporal coverage.

Despite these advantages, digital SPOT data are probably less suited to mapping natural vegetation than TM data because of their lower spectral dimensionality (most importantly, SPOT lacks midinfrared bands). The higher spatial resolution of SPOT data is useful for analyzing localized environments such as wetlands and urban areas but produces even more unwanted disaggregation of some vegetation types than TM. Also, on a per-area basis, digital SPOT data are considerably more expensive than TM data. SPOT data should be considered as an alternative only when TM data are unavailable and when the high resolution of SPOT data justify their use instead of MSS data.

Digital Image Classification

Image classification generally is accomplished by cluster analysis (often referred to as unsupervised classification) or by discriminate analysis or pattern recognition techniques (referred to as supervised classification [Moik 1982, Richards 1986]). Unsupervised classification involves clustering individual pixels into spectral classes by measured reflectance values in the original channels or in transformations of those channels. The spectral classes are then assigned to land-use and land-cover classes based on other information such as field observations, aerial photographs, and existing maps. Strahler (1981) and Franklin et al. (1986) describe an unsupervised approach to mapping forest vegetation that has been highly successful (Fig. 4).

In supervised classification, pixels are assigned to land-use and land-cover classes through a discriminant function based on spectral properties of those classes in a set of preselected training sites. Several different methods of supervised classification have been successful for mapping urban and agricultural features. These methods have not been as successful in mapping natural vegetation, because the spectral heterogeneity of classes makes specification of an adequate set of training sites difficult.

The success of image classification depends on whether land-use and land-cover

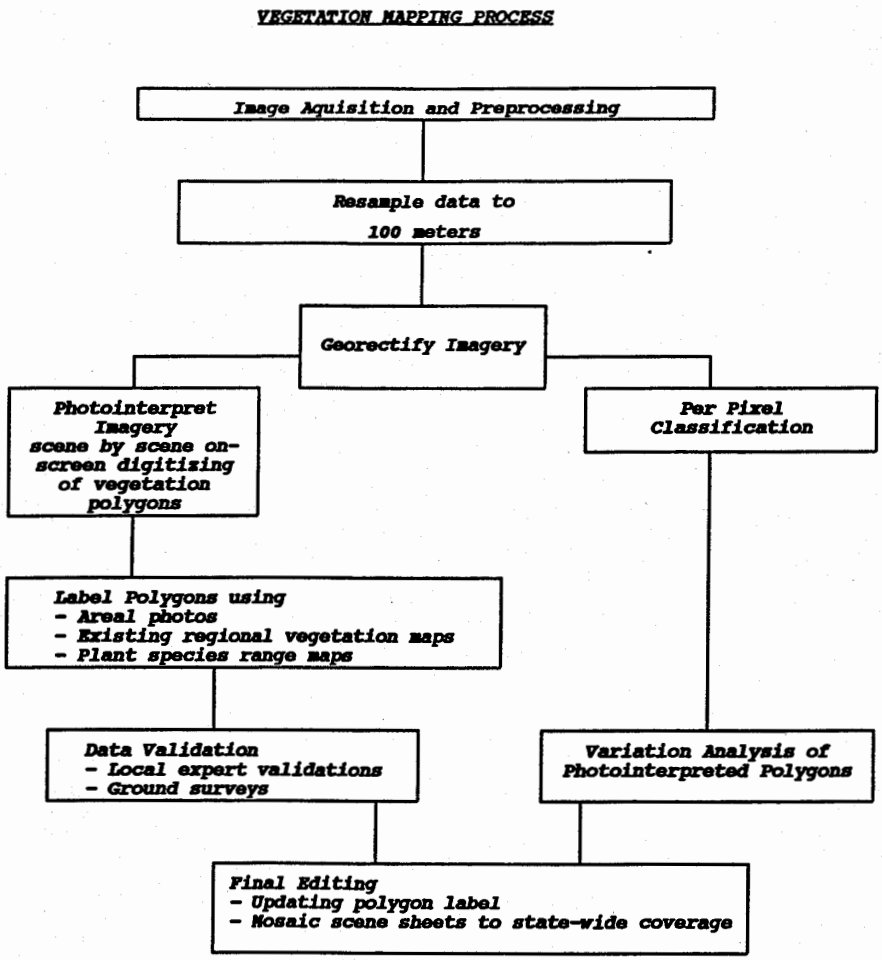

Fig. 4. Flow chart showing steps taken in unsupervised classification of digital satellite data using the FOCIS method described by Franklin et al. (1986).

classes have distinctive spectral signatures. Atmospheric corrections and band transformations often improve the ability to separate classes. High classification accuracies also may depend on incorporating ancillary cartographic information to segment the image into regions that are physically or spectrally more homogeneous. For example, digital elevation data have been used to account for illumination effects and to stratify a scene into ecological zones. Similarly, maps of soils, geology, or general land-use and land-cover patterns can be effective in segmenting imagery to improve relationships between spectral classes and land-use and land-cover classes.

Visual Interpretation of Satellite Imagery

Visual interpretation of satellite imagery entails drafting polygons onto printed image products (typically false-color composites). The process is much the same as photointerpretation of aerial photography because the analyst relies on perceived differences in image tone, texture, and context to delineate polygons. The main differences are the much lower effective resolution of satellite imagery than aerial photographs and lack of stereoviewing. Many features used by photointerpreters to identify land-use and land-cover types

(e.g., canopy spacing and height, building shape and arrangement, hillslope form) are not discernible in satellite imagery. Thus, whereas polygon boundaries often can be placed with high accuracy, polygon labeling generally requires subsequent analysis of recent aerial photographs, reliable land-use and land-cover maps, or field investigation.

Several methods have been used to manually produce land-use and land-cover maps with satellite data. Davis et al. (1989), for example, used 1:250,000 TM images to map land-use and land-cover over 2.4 million ha of southern California. They drafted polygons onto clear mylar overlays and then digitized them using ARC/INFO Geographic Information System software (ERSI, 380 New York Street, Redlands, CA 92373). Polygons were labeled by enlarging the mylar overlay to the scale of recent National High Altitude Photography, overlaying the polygons on the photos, and labeling them by photointerpretation with a stereoviewer. Vegetation boundaries that were mapped incorrectly on the satellite image were edited and incorporated into the final digital map.

Most manual mapping with satellite data is performed with standard film products that already have been radiometrically and geometrically rectified. These products are not optimally suited to mapping heterogeneous natural vegetation, especially in areas of high relief. Problems such as terrain shadowing and poor spectral separation of cover types often can be overcome with appropriate ratios and image segmentation and density slicing techniques. This requires the purchase of digital data and depends on facilities for producing high-quality film or paper output.

Vegetation Mapping Strategies for Gap Analysis

Building on experiences from the 2 Gap Analysis pilot programs (Idaho and Oregon), standardized approaches to vegetation mapping are being developed that use high quality LANDSAT Thematic Mapper digital imagery as a basic data source. Vegetation polygons are delineated by visual photointerpretation or unsupervised classification of the digital imagery. Ancillary large-scale vegetation maps and NASA high-altitude aerial photography are used to improve the accuracy of polygon labeling. In the Arizona desert, application of video photography from low-altitude aircraft is proving useful for labeling areas that have sparse vegetation cover. Within-polygon variation is assessed through analysis of the digital image. These hybrid approaches to vegetation mapping are being developed for the California Gap Analysis at the University of California, Santa Barbara and for the Arizona Gap Analysis at the University of Arizona.

In the California approach (Fig. 5), all imagery is obtained in a Universal Transverse Mercator geo-referenced format at a 25-m resolution, then resampled to the Albers equal-area projection with a 100-m resolution. During visual photointerpretation, the images are used as a backdrop plane using the Image Integrator process in ARC/INFO, while arcs are digitized on screen to delineate areas of relatively homogeneous vegetation cover. Three bands of data are used to produce a false-color infrared image: band 4 in the red plane, band 5 in the green plane, and band 3 in the blue plane. This is an intuitive color arrangement for photointerpreters accustomed to interpreting false-color infrared film images for vegetation identification and is useful for distinguishing types of vegetation by the shade or intensity of the red color produced.

The scenes are interpreted in ARCEDIT (a software program in ARC/INFO for editing map layers) using a digitizing tablet to direct an onscreen cursor over the image. Because of the ability to magnify a scene to any level required, it is possible to achieve high cartographic accuracy while producing a small-scale map. Displaying each 100-m pixel so that it is 1 to 2 mm on a side facilitates interpretation.

Although visual image interpretation can be very subjective, it offers several advantages over standard unsupervised classification. It is possible to map both areas of

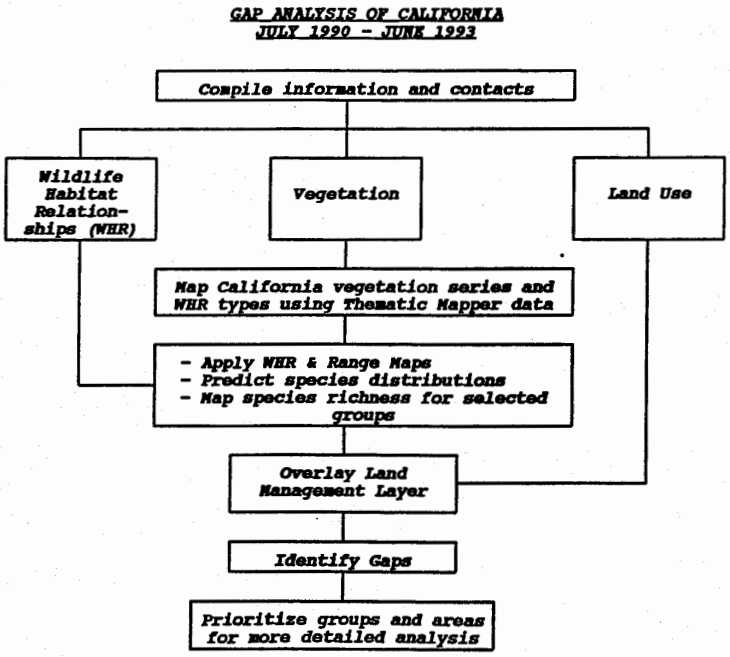

Fig. 5. Flow diagram showing the steps followed in California for developing a vegetation map from satellite imagery.

high homogeneity and areas with strong mosaic patterns. Color and texture are the most useful tools for delineating both types of areas. A single, local area might have several polygons that vary only by the percentage composition of the same or similar vegetation types. If 2 adjacent polygons are determined to have identical vegetation, and the differences observed in the satellite imagery are the result of differing substrates or canopy closure, then those polygons can be merged in the final editing process after they are labeled. Unsupervised classification of the digital imagery superimposed on the polygon map is used to provide a quantitative estimate of spatial heterogeneity.

Because mapping for Gap Analysis is at a landscape scale, few polygons will be homogeneous. Rather than attempting to assign a single vegetation type to a polygon, it is often preferable to assign both primary and secondary attributes. An attribute table may include information on the percentage of the polygon represented in each class, the canopy closure of the stand, and the presence of wetlands or disturbances. Aerial photography is examined for every polygon and an interpretation of vegetation cover type is made based on these images as well as on paper maps.

All data layers used in mapping are stored in the Albers equal-area projection, but can be transformed into other projections (e.g., Lambert's equal-area projection) as needed for regional mapping. Ancillary, state-wide vector data layers used for image interpretation are divided into digital files whose boundaries correspond to those of 1:250,000 USGS topographic map quadrangles. As the vegetation map is processed, it is stored as a single, continuous state-wide coverage. This practice eliminates the need for edge-matching after image interpretation and allows the entire map to be easily accessed and queried.

Other states, such as Utah and Arizona, are carrying out unsupervised classification of digital TM imagery to identify groups of pixels with similar spectral signatures. These areas are converted to vector files, and ancillary data (large-scale local vegetation maps, low-altitude aerial

video images, etc.) are used to attach vegetation type labels to the polygons. Mapping methods vary from state to state, in response to the variety and characteristics of local vegetation cover types.

PREDICTING ANIMAL DISTRIBUTIONS AND SPECIES RICHNESS

Traditional Approaches to Mapping Species Distributions

Many natural history accounts use maps to illustrate species distribution. Although these maps are drawn to many different scales, most are extremely small scale, depicting the range of a species within the confines of a field-guide format. Due to scale limitations, inappropriate habitat within the distribution of a species is not excluded. The user must be aware of this generalization and should expect a species to be present only in suitable habitat within the depicted range.

Four types of traditional distribution maps exist: (1) dot distribution maps, (2) grid-based maps, (3) hybrid dot distribution and range maps, and (4) range maps. Traditional distribution maps are based on the localities of observations or specimens. The simplest way to illustrate the presence of a species at a particular place is with a dot on a map. The dot covers a much larger area than the home range of the actual specimen. Dot distribution maps become more useful as records are added, ultimately forming a pattern that approaches a range map. Because dot maps only show where a species has been seen in the past, their accuracy declines with distance from the localities represented by the dots. Their accuracy also is not good when older locality data are used to describe distributions in areas with recent human activity that has affected the occurrence of vegetation. Blank areas on a dot distribution map do not necessarily mean a species is absent but merely that no records were available.

A modification of the dot distribution map places a symbol in the center of a geographic unit if a species occurs anywhere within that unit. These units are small political or administrative districts (like counties) or cells of a grid (Udvardy 1981). Maps showing the occurrence of bird species in cells of 1 degree latitude by 1 degree longitude have been prepared for many states (e.g., Stephens and Sturts 1991). In Great Britain, extensive inventory information has been compiled into atlases that depict presence of species (e.g., birds and plants) within 10 × 10-km grid cells. Breeding bird atlases also are being prepared for many U.S. states and some Canadian provinces (e.g., Cadman et al. 1987). Grid maps share the limitations of dot maps and, especially where the grid cell is large, provide less information about the actual locality of the specimen record.

Hybrid dot distribution and range maps, as in *Mammals of Maryland* (Paradiso 1969) (Fig. 6), show localities of individual specimen records but enclose them within a boundary. *The Mammals of North America* (Hall 1981) represents a variation of this approach, only showing records at the periphery of the range. A hybrid dot and range map predicts the presence of a species in areas within the range boundaries devoid of specimen records. Rarely are areas of unsuitable habitat excluded from either hybrid dot and range maps or range maps. A range map usually is based on specimen locality records, but these are not shown on the map. Range maps and hybrid dot and range maps often use boundaries of major biomes (forests, deserts) to determine range limits. In the final analysis, all forms of distribution maps are probability statements about the presence of a species in an area, and their predictive powers are scale dependent.

Habitat-based Distribution Prediction

Vertebrate biologists have long used knowledge of an animal's habitat to predict its presence or absence (Baker 1956, Armstrong 1972). Using vegetation to predict the distribution of species has a number of limitations, but also avoids many

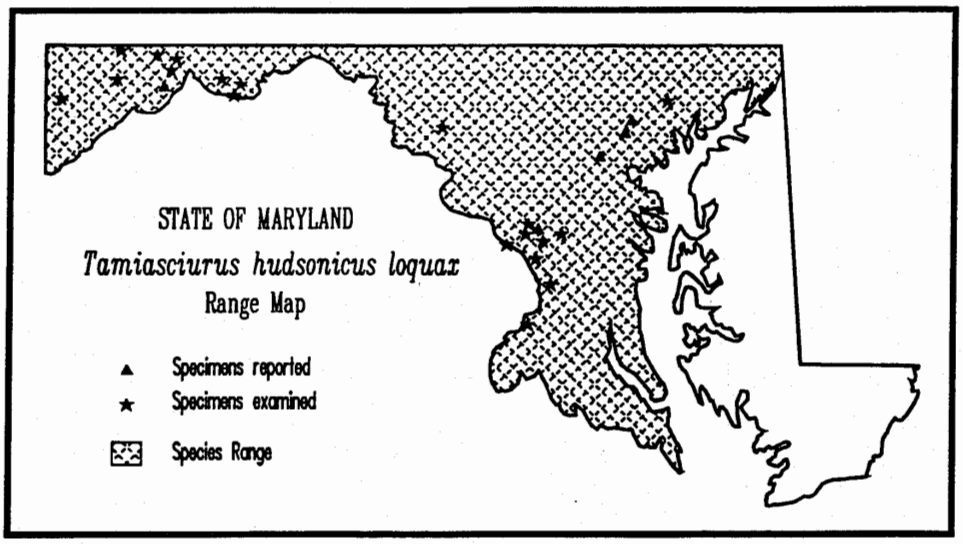

Fig. 6. Hybrid dot and range map (adapted from *Mammals of Maryland*, Paradiso 1969).

pitfalls of traditional mapping. Because the process does not draw directly on specimen locality records, unexplored regions of suitable habitat within the overall range limits are included in the range. Conversely, areas of unsuitable habitat are excluded from the predicted distribution. Depending on the habitat specificity of the species, the map can be a refined prediction of distribution.

For example, in the western United States, heteromyid rodents such as pocket mice (*Perognathus* spp., *Chaetodipus* spp.), kangaroo rats (*Dipodomys* spp.), and kangaroo mice (*Microdipodops* spp.) occur in deserts, grasslands, and chaparral. They barely enter the pinyon–juniper zone and do not occur in forests, broadleaf woodlands, wetlands, or subalpine and alpine habitats. Conversely, many microtine rodents (e.g., *Microtus* spp.) occur only in grasslands and meadows of forested mountain ranges; many of these ranges are now surrounded by desert. Presumably these microtines reached these localities during geologic periods of higher rainfall when these mesic habitats were more widespread. Traditional range maps (Fig. 7) (Bailey 1936) for such different species as the Great Basin pocket mouse (*Perognathus parvus*) and the long-tailed vole (*Microtus longicaudus*) show considerable range overlap, although the 2 species would not be syntopic in the wild.

Several factors complicate the use of vegetation to predict the presence of a species. In many cases, birds respond more to the structure of vegetation than to floristic composition (Miller 1951, Cody 1985), although examples exist of birds responding to the presence of a particular tree or shrub species (e.g., Holmes and Robinson 1981). Ideally, the degree of canopy closure, spacing of dominant trees or shrubs, height of dominant trees and shrubs, and height differential between canopy and understory layers should be addressed in habitat descriptions.

Species differ in the breadth of their habitat requirements. A few species, like coyotes (*Canis latrans*) and deer mice (*Peromyscus maniculatus*), are generalists. Others, like the sage grouse (*Centrocercus urophasianus*), are restricted to a narrow range of vegetation types. Most species occur in several vegetation types, but usually can be associated with major vegetation groupings (e.g., coniferous forests, grasslands, desert shrub land, riparian woodlands, marshes, etc.). Some species have different habitat requirements in different parts of their range, and national or

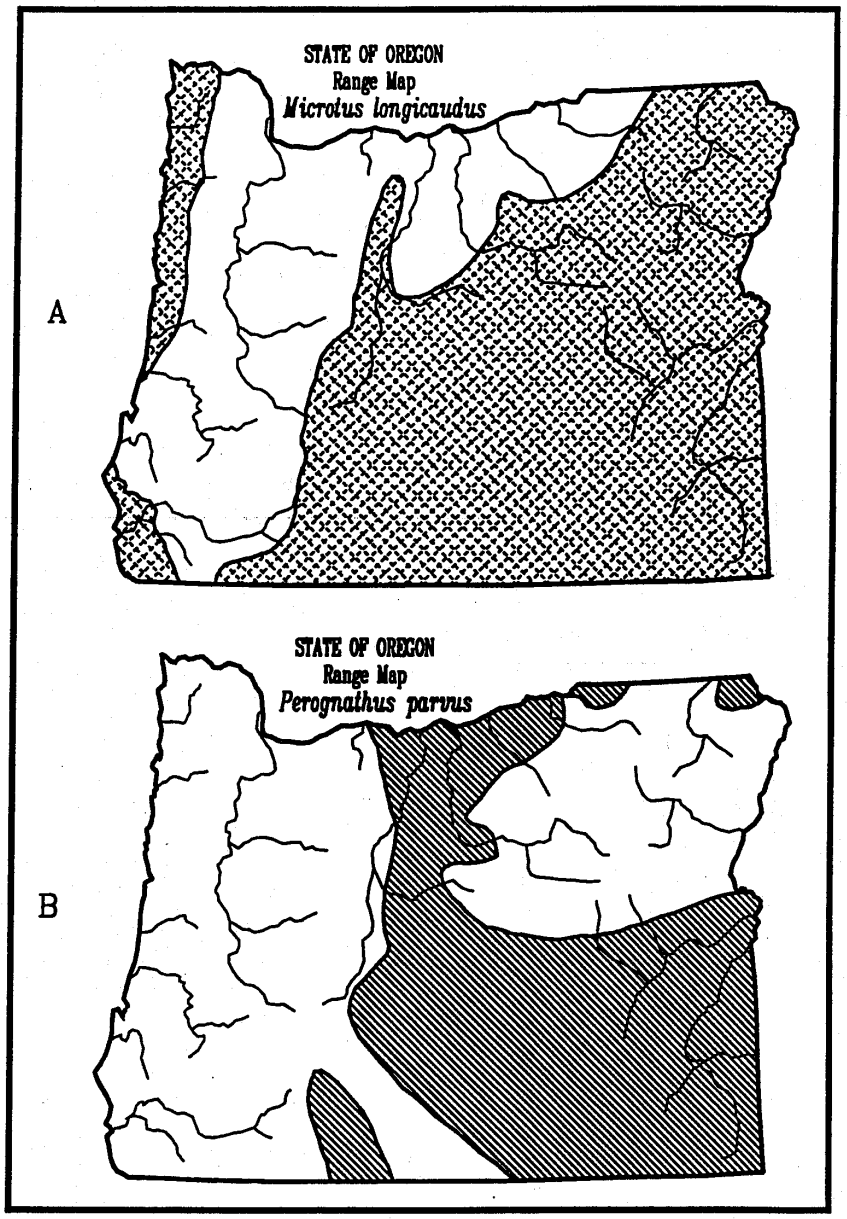

Fig. 7. Small-scale distribution maps of *Microtus longicaudus* (A) and *Perognathus parvus* (B) in Oregon (adapted from Bailey 1936). Note areas of overlap.

regional guides usually do not reflect the narrower range of habitats occupied by a species in any particular state. For example, "throughout its wide range in the western United States the Ash-throated Flycatcher" (*Myiarchus cinerascens*) "occurs in quite varied habitat, but in Idaho is restricted to the arid juniper-covered ridges that occupy a rather limited area on the southern edge of the state" (Burleigh 1972:212).

Recent efforts to classify vegetation in the western United States have resulted in detailed descriptions of plant associations. For example, Baker (1984) recognizes 403 plant associations in Colorado, and Holland (1986) recognizes 375 natural communities (which usually describe a higher

level in the vegetation classification hierarchy than the association) in California. Many units of a vegetation classification at this level of detail share dominant species and structure but differ in ratio of dominant species or presence of certain understory species. Although they are of interest to phytosociologists, these differences may not be important to most animals (invertebrates with strong relationships to particular host plants would be an exception). Thus, the 375 natural communities in California were cross-referenced to 53 wildlife habitat types by Mayer and Laudenslayer (1988).

Because no 2 stands of vegetation are exactly alike, any vegetation classification is an abstraction of the real world, and determination of which level in the vegetation classification hierarchy best reflects differences in animal communities is difficult (Scott et al. 1989). In most cases, an animal habitat classification lumps vegetation types because the ability of plant ecologists to differentiate between plant communities exceeds the ability of animal ecologists to detect differences in animal response to various plant communities. Alternately, animal species do not respond to all the vegetation differences noted by plant ecologists; rather they respond similarly to plant communities with similar life forms (Miller 1951). Therefore, plant communities with similar animal species are combined into 1 animal habitat type. Following the example of Mayer and Laudenslayer (1988), Gap Analysis groups structurally and floristically similar vegetation associations into broader habitat categories for data bases describing the association of species and habitat types. In Idaho, for example, 119 vegetation cover types were generalized into 33 broader habitat types (Table 2). Table 3 shows the predicted presence or absence of Idaho's shrews (Soricidae) in these habitat types.

Data Sets Describing General Distribution

Although best known for their computerized data bases on rare and endangered plants and animals, state natural heritage programs also have been building data bases of more general information on nonendangered species and plant communities. Data bases for vertebrates are called Vertebrate Characterization Abstracts (VCA's) and contain state-specific distribution and ecological information for each species. The VCA's are a family of microcomputer-compatible data bases. Among this family of data bases are distributional checkoffs that indicate the presence or absence of a species in each county, ecoregion, and major watershed (defined as hydrologic accounting units of the U.S. Geological Survey) in the state.

Because they are usually compiled from general references, VCA's usually contain some inaccuracies in areas where the fauna is poorly known. In western North America, VCA-state data bases have been completed in Idaho, Montana, and Oregon. The Oregon data base differs from the other 2 in that physiographic provinces have been substituted for the ecoregions as a distributional checkoff.

Colorado and Utah have detailed data bases with information on the ecology and distribution of their vertebrate species (Multi-State Fish and Wildlife Information Systems, Dep. Fish. and Wildl. Sci., Virginia Polytechnic Institute and State Univ., Blacksburg, Va.). Although similar in concept to the VCA, the Multi-State data base contains more detailed tabular information. The geographic portions of these data bases also lend themselves to GIS production of predicted distribution maps. The State of California developed its own wildlife information retrieval system (Airola 1988), intermediate in detail between the VCA and the Multi-State data bases. Small-scale range maps with distributional limits of terrestrial vertebrates in the state also are available.

Associating Animal Species with Habitats

Condensed information about species' habitat preferences can be found in national reference works. For example, The American Ornithologists' Union *Check-list of North American Birds* (Am. Ornith.

Table 2. Grouping of Idaho actual vegetation types into Idaho wildlife habitats.

	Wildlife habitat	Mapping unit code	Graphics	Vegetation type name[a]
1	Alpine	6	ALP	Alpine communities
2	Whitebark pine forests	13A	SF2	*Pinus albicaulis* (*Abies lasiocarpa*)
		13B	SF2	*Pinus albicaulis, Pinus contorta*
3	Subalpine fir, spruce, and mountain hemlock forests and woodlands	11A	SF1	*Picea engelmannii, Abies lasiocarpa*
		12	SF1	*Abies lasiocarpa*
		12A	SF1	*Abies lasiocarpa* (*Pinus contorta, Populus tremuloides*)
		12B	SF1	*Abies lasiocarpa* (*Pseudotsuga menziesii, Populus tremuloides*)
		12C	SF1	*Abies lasiocarpa* (*Pinus albicaulis, Picea engelmannii*)
		12D	SF1	*Abies lasiocarpa* (*Pinus albicaulis*)
		12E	SF1	*Abies lasiocarpa* (*Pinus contorta*)
		12F	SF1	*Abies lasiocarpa* (*Pseudotsuga menziesii*)
		12G	SF1	*Abies lasiocarpa* (*Picea engelmannii*)
		12H	SF1	*Abies lasiocarpa* (*Pinus contorta, Picea engelmannii*)
		12I	SF1	*Abies lasiocarpa* (*Tsuga mertensiana, Pinus contorta*)
		12J	SF1	*Abies lasiocarpa* (*Tsuga mertensiana–Picea engelmannii*)
		27A	SF3	*Tsuga mertensiana* (*Pseudotsuga menziesii*)
		27B	SF3	*Tsuga mertensiana* (*Abies lasiocarpa–Picea engelmannii*)
4	Subalpine lodgepole pine forests	10A	SF4	*Pinus contorta, Populus tremuloides* (*Abies lasiocarpa*)
		10B	SF4	*Pinus contorta, Abies lasiocarpa*/mountain brush
		10H	SF4	*Pinus contorta, Abies lasiocarpa*
		10I	SF4	*Pinus contorta, Picea engelmannii*
		10J	SF4	*Pinus contorta* (*Abies lasiocarpa–Picea engelmannii*)
		10N	MF5	*Pinus contorta*/brush
5	Montane lodgepole pine forests	10	MF5	*Pinus contorta*
		10D	MF5	*Pinus contorta, Pseudotsuga menziesii*
		10K	MF5	*Pinus contorta* (*Abies grandis–Larix occidentalis*)
		10L	MF5	*Pinus contorta* (*Abies grandis–Pseudotsuga menziesii*)
		10M	MF5	*Pinus contorta* (*Pinus monticola, Pseudotsuga menziesii*)
		10P	MF5	*Pinus contorta* (*Larix occidentalis, Pseudotsuga menziesii*)
		R5	RIP	*Pinus contorta* floodplain riparian
6	Lodgepole pine woodlands	10C	MF5	*Pinus contorta, Populus tremuloides*/mountain brush
		10E	MF5	*Pinus contorta, Pseudotsuga menziesii, Populus tremuloides*
		10G	MF5	*Pinus contorta*/*Artemisia tridentata* ssp. *vaseyana*
7	Cedar and hemlock forests	25A	MF1	*Pinus monticola–Thuja plicata* (*Abies grandis–Pseudotsuga menziesii*)
		25B	MF1	*Pinus monticola–Thuja plicata* (*Pinus contorta*)

Table 2. Continued.

	Wildlife habitat	Mapping unit code	Graphics	Vegetation type name[a]
		25C	MF1	*Pinus monticola–Thuja plicata (Larix occidentalis–Pseudotsuga menziesii)*
		25D	MF1	*Pinus monticola–Thuja plicata (Pseudotsuga menziesii)*
		25E	MF1	*Pinus monticola, Pinus ponderosa, Pseudotsuga menziesii, Larix occidentalis (Tsuga heterophylla–Abies grandis)*
		25F	MF1	*Pinus monticola, Pseudotsuga menziesii (Larix occidentalis, Tsuga heterophylla–Abies grandis)*
		28A	MF1	*Thuja plicata–Abies grandis (Pinus monticola)*
		28B	MF1	*Thuja plicata–Tsuga heterophylla (Pseudotsuga menziesii, Pinus monticola)*
		29A	MF1	*Tsuga heterophylla–Abies grandis (Larix occidentalis)*
		29B	MF1	*Tsuga heterophylla–Abies grandis (Pseudotsuga menziesii)*
8	Grand fir forests	24A	MF2	*Abies grandis (Pseudotsuga menziesii)*
		24B	MF2	*Abies grandis (Pseudotsuga menziesii, Pinus contorta)*
		24C	MF2	*Abies grandis (Thuja plicata–Pseudotsuga menziesii)*
		24D	MF2	*Abies grandis (Pinus contorta, Larix occidentalis)*
		24E	MF2	*Abies grandis (Pseudotsuga menziesii–Pinus monticola)*
		24F	MF2	*Abies grandis (Pseudotsuga menziesii, Larix occidentalis)*
		25B	MF1	*Pinus monticola–Thuja plicata (Pinus contorta)*
9	Western larch forests	25A	MF1	*Pinus monticola–Thuja plicata (Abies grandis–Pseudotsuga menziesii)*
		25B	MF1	*Pinus monticola–Thuja plicata (Pinus contorta)*
		26C	MF1	*Larix occidentalis–Pinus contorta (Pseudotsuga menziesii, Tsuga heterophylla)*
		26D	MF1	*Larix occidentalis, Abies grandis (Pseudotsuga menziesii, Pinus monticola)*
10	Douglas-fir forest	9	MF2	*Pseudotsuga menziesii*
		9E	MF2	*Pseudotsuga menziesii (Populus tremuloides, Pinus contorta)*
		9F	MF2	*Pseudotsuga menziesii (Pinus contorta)*
		9H	MF2	*Pseudotsuga menziesii (Picea engelmannii)*
		9J	MF2	*Pseudotsuga menziesii (Pinus contorta, Larix occidentalis)*
		9L	MF2	*Pseudotsuga menziesii, Abies grandis (Pinus ponderosa)*
		9M	MF2	*Pseudotsuga menziesii (Abies grandis–Larix occidentalis)*
		9N	MF2	*Pseudotsuga menziesii (Abies grandis–Thuja plicata)*
		9Q	MF2	*Pseudotsuga menziesii (Larix occidentalis)*
		9R	MF2	*Pseudotsuga menziesii (Pinus ponderosa–Larix occidentalis)*

Table 2. Continued.

	Wildlife habitat	Mapping unit code	Graphics	Vegetation type name[a]
		9S	MF2	*Pseudotsuga menziesii* (*Pinus ponderosa–Pinus monticola*)
		9T	MF2	*Pseudotsuga menziesii–Larix occidentalis* (*Pinus monticola, Pinus contorta*)
11	Douglas-fir forests and woodlands	9A	MF2	*Pseudotsuga menziesii* (*Pinus flexilis*)/mountain brush
		9B	MF2	*Pseudotsuga menziesii, Populus tremuloides/Artemisia tridentata* ssp. *vaseyana*
		9C	MF2	*Pseudotsuga menziesii, Populus tremuloides*/mountain brush
		9D	MF2	*Pseudotsuga menziesii/Artemisia tridentata* ssp. *vaseyana*
		9G	MF2	*Pseudotsuga menziesii, Pinus flexilis, Pinus albicaulis*
		9I	MF2	*Pseudotsuga menziesii* (*Pinus ponderosa*)
12	Ponderosa pine forests and woodlands	8A	MF3	*Pinus ponderosa* (*Pseudotsuga menziesii*)
		8B	MF3	*Pinus ponderosa/Artemisia tridentata* ssp. *vaseyana*
		8C	MF3	*Pinus ponderosa, Pinus contorta*
		8D	MF3	*Pinus ponderosa*/bunchgrass
		8E	MF3	*Pinus ponderosa, Pseudotsuga menziesii*/bunchgrass
		7A	WD2	*Pinus flexilis/Sarcobatus vermiculatus*
		7B	WD2	*Pinus flexilis/Purshia tridentata*
14	Juniper woodlands	5A	WD2	*Juniperus occidentalis/Artemisia arbuscula*
		5B	WD2	*Juniperus occidentalis/Artemisia tridentata* ssp. *vaseyana*
		5C	WD2	*Juniperus osteosperma/Artemisia tridentata* ssp. *vaseyana*
		5D	WD2	*Juniperus osteosperma* (*J. scopulorum*)/*Artemisia tridentata*
		22	WD2	*Pinus monophylla–Juniperus osteosperma*
15	Mountain brush	18	MBR	Mountain brush
16	Brushfields	BR	BR	Brushfields
17	Clearcuts	C	CUL	Recent timber harvests
18	Mountain big sagebrush with trees	17B	TS2	*Artemisia tridentata* ssp. *vaseyana, Artemisia arbuscula/Pinus contorta, Populus tremuloides*
		17C	TS2	*Artemisia tridentata* ssp. *vaseyana/Pseudotsuga menziesii, Populus tremuloides*
		17D	TS2	*Artemisia tridentata* ssp. *vaseyana/Pseudotsuga menziesii*
		17E	TS2	*Artemisia tridentata* ssp. *vaseyana/Abies lasiocarpa*
		17F	TS2	*Artemisia tridentata* ssp. *vaseyana/Populus tremuloides*
		17G	TS2	*Artemisia tridentata* ssp. *vaseyana/Pinus ponderosa*
19	Mountain big sagebrush without trees	17	TS2	*Artemisia tridentata* ssp. *vaseyana, Purshia tridentata*
		17A	TS2	*Artemisia tridentata* ssp. *vaseyana, Artemisia arbuscula*
		21B	LS	*Artemisia arbuscula, Artemisia tridentata* ssp. *vaseyana*

Table 2. Continued.

	Wildlife habitat	Mapping unit code	Graphics	Vegetation type name[a]
20	Tall sagebrush	15A	TS1	*Artemisia tridentata, Artemisia arbuscula*
		15B	TS1	*Artemisia tridentata* lava fields
		16	TS1	*Artemisia tripartita*
21	Low sagebrush with trees	21A	LS	*Artemisia arbuscula/Juniperus occidentalis*
22	Low sagebrush without trees	20	LS	*Artemisia longiloba*
		21C	LS	*Artemisia arbuscula, Artemisia tridentata*
		21D	LS	*Artemisia arbuscula, Artemisia nova*
		21E	LS	*Artemisia arbuscula, Artemisia frigida*
23	Salt desert shrub	19	SDS	Salt desert shrub
24	Canyon grassland	23	GRS	Canyon grasslands
25	Non-native grasslands	2	CUL	Perennial bunchgrass seedings
		3	CUL	Annual grasslands
26	Marsh	4	RIP	*Scirpus acutus* (*Typha latifolia*) marsh
27	Canyon shrub riparian	R1	RIP	Canyon shrub riparian
28	Cottonwood riparian	R2	RIP	*Populus trichocarpa* floodplain riparian
		R3	RIP	*Populus angustifolia* floodplain riparian
29	Willow riparian	R4	RIP	*Salix* ssp. floodplain riparian
30	Sand dunes	SAND	MBR	Sand dune communities
31	Agriculture	1	CUL	Agricultural crop land and pasture land
32	Urban and industrial	U/I	CUL	Urban and industrial
33	Open water	OW		

[a] Structural layers in vegetation types are separated by a "/." Within a layer, relative dominance relationships between or among species are indicated by parentheses, commas, or dashes: parentheses distinguish between dominant species and major species with less canopy coverage; commas signify codominant species that tend to occur in pure stands; a dash signifies codominant species that tend to occur in mixed stands.

Union 1983) contains concise statements about bird habitats that often mention preferences for specific vegetation types. The 2 standard national reference works on butterflies of North America (Howe 1975, Scott 1986) describe both general habitat types and specific host plants for larvae. When coverage is available, Mammalian Species, a series published by the American Society of Mammalogists, usually provides good habitat descriptions based on a review of original literature. For some regions, field guides (such as the *Field Guide to Western Reptiles and Amphibians* [Stebbins 1985]) contain the most detailed descriptions of habitat preferences that are available.

Nearly every state has books describing the natural history and distribution of various classes of vertebrates and has 1 or more bird books, often written for a nontechnical audience. These texts differ in age, quality, and depth of coverage, but often are quite helpful. Books on state mammal faunas tend to be written for a scientific audience. Few states have books on their herpetofauna, but, where they do, the treatment is usually at a technical level. Because little is known about the ecology of many smaller, inconspicuous species, their habitat preferences are often extrapolated from limited studies or from studies of closely related species. The U.S. Forest Service (USFS) has published manuals describing the relationships between wildlife and habitat in several areas (e.g., DeGraaf and Rudis 1986).

GIS Models of Species Distributions

Much past and current research in wildlife biology focuses on describing habitats of various species. Starting in the 1970's,

Table 3. Association between Idaho shrews (*Sorex*) and habitat types: 1 = present, 0 = absent.

Habitat[a]	Masked shrew (*Sorex cinereus*)	Preble's shrew (*S. preblei*)	Vagrant shrew (*S. vagrans*)	Dusky shrew (*S. monticolus*)	Water shrew (*S. palustris*)	Merriam's shrew (*S. merriami*)	Pygmy shrew (*S. hoyi*)
1	1	0	0	1	1	0	0
2	0	0	0	1	1	0	1
3	1	0	1	1	1	0	1
4	1	0	1	1	1	0	1
5	1	0	1	1	1	0	1
6	1	1	1	1	1	0	1
7	1	0	1	1	1	0	1
8	1	0	1	1	1	0	0
9	1	1	1	1	1	1	0
10	1	0	1	1	1	0	0
11	0	0	1	0	0	1	0
12	0	1	1	0	0	1	0
13	0	0	1	0	0	1	0
14	1	0	1	0	1	0	1
15	0	0	1	0	0	0	1
16	0	1	1	0	1	1	0
17	0	1	1	0	0	1	0
18	0	1	1	0	0	1	0
19	0	1	1	0	0	1	0
20	0	1	1	0	0	1	0
21	0	0	0	0	0	1	0
22	0	0	1	0	1	0	0
23	0	0	0	0	0	0	0
24	1	1	1	0	0	0	0
25	0	1	1	0	0	0	0
26	0	1	1	0	0	0	0
28	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0

[a] Habitats are listed in Table 2.

this information has been used to produce wildlife–habitat-relationship models (e.g., Thomas 1979). These models use quantified indices of habitat suitability to predict wildlife population response to habitat change (Verner et al. 1986). These are not spatial models, but they can be applied to individual management units. Given knowledge of the geographical limits of a species' distribution, its ecological limiting factors, and its habitat preferences, a GIS can be used to predict its distribution. Used in this fashion, a GIS can provide a spatial frame of reference for traditional wildlife–habitat-relationship models by applying the models to polygons of a vegetation cover-type map.

A minimum of 4 sets of information is required for the generation of GIS maps predicting a species' distribution: (1) a digital map of vegetation cover types or animal habitat types, (2) a digital map of the study area divided into geographic units such as counties or a grid system, (3) a data base indicating the presence or absence of a species in each of the geographic units, and (4) a data base predicting the presence or absence of each species in each vegetation or habitat type. In Idaho, additional data bases were developed to increase the correspondence between predicted and known distributions. These included digital maps of climate, potential vegetation, hydrology, and wetlands.

Before developing a GIS-based model of vertebrate species distributions, 2 scale-related issues deserve special consideration. First, the desired scale of analysis must

be established prior to development of the GIS data base and distribution models (as described above). Second, the scale of available animal–habitat-relationship information may not correspond to the GIS data base. Existing habitat-relationship models often describe microhabitat needs and seral stage preferences for a species. The minimum mapping unit for GIS vegetation cover maps is larger than these features, so important habitat components will be unaddressed or described more generally as polygon attributes. The fact that most vertebrate species are not well studied and their habitats are not well known creates a different type of limitation. Detailed habitat-relationship information is available for only a few well-studied species, usually game species. Statements such as "lives in coniferous forests" are typical habitat descriptions for many smaller species. For a large-scale Gap Analysis (e.g., state or ecoregion), this scarcity of information reduces the accuracy of distribution prediction.

In the simplest case, predicted distribution maps are developed by overlaying the vegetation map layer with the geographic unit layer. Each polygon is assigned a vegetation type and a county. Each species is assigned to each polygon as an attribute. Internal relationships between the combined map layers and the vegetation association and county-of-occurrence matrices are created in the GIS. An automated iterative process codes each species for 1 as present or 0 for absent in each polygon based on the relational data bases. The result is a single map layer with several hundred attributes attached to each polygon, each attribute being a vertebrate species.

This procedure avoids creating several hundred separate map layers, one for each species. Using the GIS, the predicted distribution of each species can be displayed individually or used in tabular output. Any desired combination of species can be summed to calculate the species richness in each polygon.

In Idaho, the predicted distributions for a sample of 14 vertebrate species were compared with known distributional data. Each species' distribution was initially defined by 3 different models: (1) county-of-occurrence and vegetation association, (2) ecoregion-of-occurrence and vegetation association, and (3) traditional range map and vegetation association. For widely distributed species, such as elk (*Cervus elephus*) and western meadowlark (*Sturnella neglecta*), all 3 models produced similar results. However, for species with restricted distributions, the ecoregion and traditional range map models overestimated their distribution. The county-of-occurrence model provided the best results for these species. This model assumed that if a species was present in a county, then it was present in all appropriate vegetation polygons that were intersected by that county, including portions of those polygons extending into adjacent counties.

We ran the county-of-occurrence model on all terrestrial vertebrates (waterfowl and wetland-associated species were omitted) and compared predicted species lists with documented species lists for 3 managed areas (Table 4). The results indicated that for most terrestrial vertebrates the county-of-occurrence and vegetation model worked well. However, several weaknesses were identified. First, reptile distribution was poorly predicted by vegetation, probably because reptiles respond strongly to climate. Omission error was low and commission error high for reptiles (Table 4). That is generally less true for birds but true again for mammals. Second, species closely associated with hydrologic features were grossly overestimated. Predicting their distribution required use of a hydrologic data layer. Third, fossorial rodents, such as pocket gophers and ground squirrels, were overestimated, suggesting that our vegetation map is not integrating soils characteristics important in determining rodent distribution or that we need to adjust the vegetation associations assigned to fossorial rodents. Fourth, competition among the 3 pocket gopher species may be taking place on a microhabitat scale and complicates regional scale-mapping. Finally, rare species with local distributions

Table 4. Comparison of initial county-of-occurrence and vegetation association distribution model with species lists from 3 managed areas. Omission errors (species that occurred on the site but were not predicted) include species listed as occasional or accidental. Some commission errors (species predicted but not recorded on the site) may be due to incomplete area lists.

Managed area and taxa	Area list	Omission error Count	Omission error Percent	Commission error Count	Commission error Percent
Idaho National Engineering Lab					
Amphibians	1	0	0.0	1	100.0
Reptiles	9	0	0.0	2	22.2
Birds	51	3	5.9	13	5.5
Mammals	36	4	11.1	15	41.7
Total	97	7	7.2	1	32.0
Snake River Birds of Prey Natural Area					
Amphibians	7	0	0.0	0	0.0
Reptiles	16	1	6.3	2	12.5
Birds	77	10	13.0	20	26.0
Mammals	44	7	15.9	17	38.6
Total	144	18	12.5	39	27.1
Kootenai National Wildlife Refuge					
Amphibians	7	2	28.6	2	28.6
Reptiles	6	0	0.0	0	0.0
Birds	125	16	12.8	7	5.6
Mammals	40	2	5.0	9	22.5
Total	178	20	11.2	18	10.1
Grand Total					
Amphibians	15	2	13.3	3	20.0
Reptiles	31	1	3.2	4	12.9
Birds	253	29	11.5	40	15.8
Mammals	120	13	10.8	41	34.2
Total	419	45	10.7	88	21.0

were overestimated using this method (*see* below).

An illustration of the predictive powers of distribution models is provided by the sharp-tailed grouse (*Tympanuchus phasianellus*). The sharp-tailed grouse is a well-studied species in Idaho and was believed to be rare and locally distributed. By using a combination of vegetation maps that showed the distribution of deciduous shrub and forb understory plants required by the grouse, we produced a model that predicted a distribution well beyond its known distribution. Independent inventories have recently reported sharp-tailed grouse in new areas predicted by our distribution model. Thus, GIS-based predicted distribution maps may often be more accurate than empirical data, especially for poorly surveyed regions.

Mapping Wetland and Aquatic Habitats and Species

Riparian and wetland associated species present special difficulties for Gap Analysis. Even small wetlands or riparian zones may be ecologically critical, yet delineation of these microhabitat features is impossible at the mapping scales used in regional analyses. To confront this problem, we tested 2 approaches in Idaho. First, vegetation types that commonly contain wetland habitats in Idaho were identified. Then, wetland species were assigned to those vegetation polygons. The resulting distribution maps predicted the regional distribution of aquatic- and wetland-dependent species and are comparable to the other state-wide maps. However, these maps predicated the distribution of wetland species across broad expanses of uplands (Fig. 8A, C).

We generally do not perceive wetland and riparian species occurring across the landscape as we do other species. Instead, we consider their habitats as unique. Therefore, the modeling approach described above produces unsatisfactory results, with distributions painted across large expanses of dry land. The second approach used 1:100,000-scale U.S Geological Survey Digital Line Graph (DLG) hydrography to represent streams and lakes. These data include water bodies larger than 2 ha. The entire state-wide data set was too large to effectively manipulate in subsequent analyses, even with modern computer workstations, so we eliminated the smallest order streams. Before elimination, the average distance between hydrographic features was on the order of several hundred meters; after elimination, the average distance was several kilometers. Each feature was buffered to an arbitrary distance of 200–400 m to produce a potential riparian zone.

Wetlands at a scale larger than 1:500,000 have never been mapped for the state of Idaho. We created our own wetland map layer by digitizing all the wetland symbology on the U.S. Geological Survey 1:100,000-scale maps of the state. We sup-

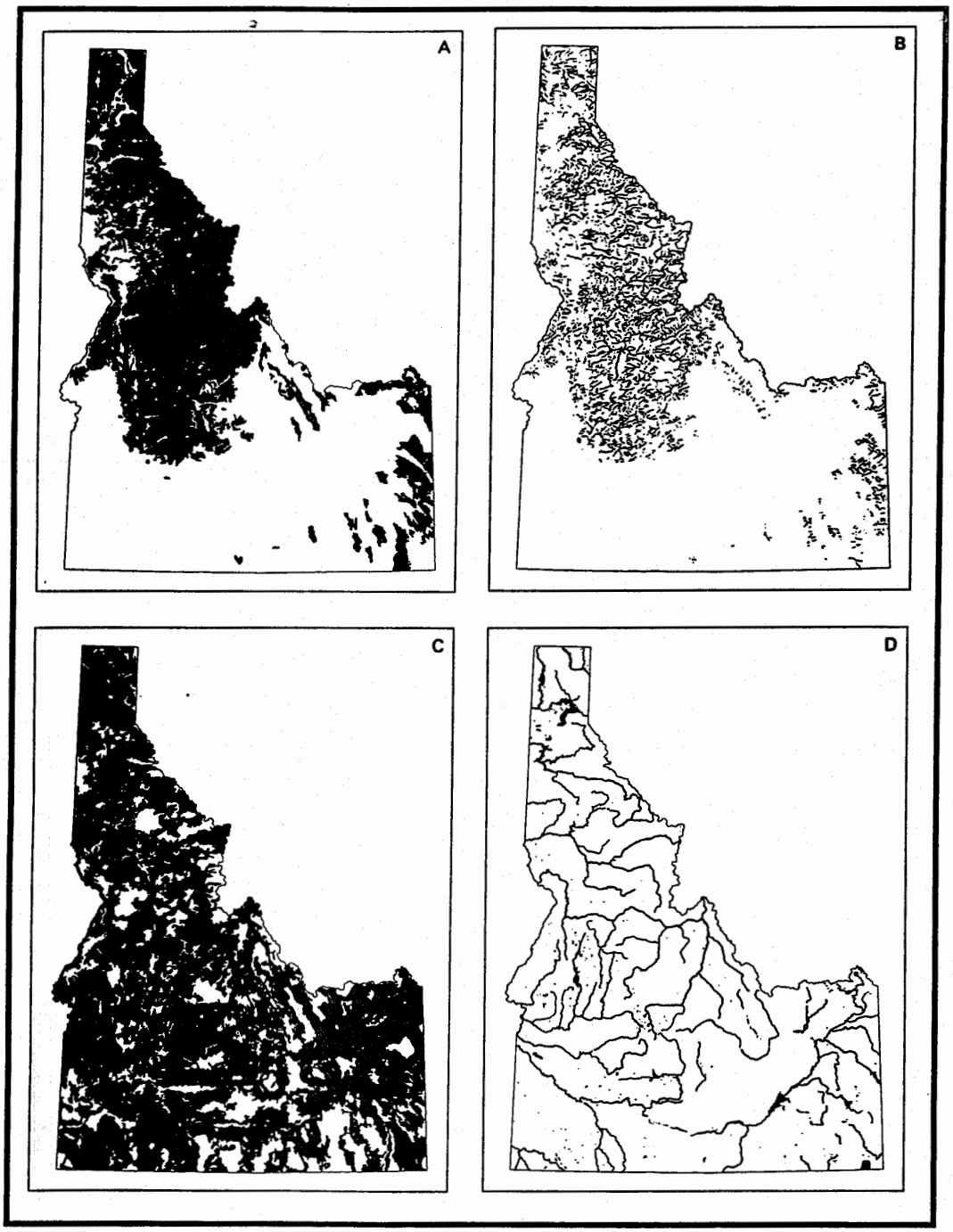

Fig. 8. Regional versus digital line graph methods used to predict wetland and aquatic species: (A) predicted regional distribution of American dipper; (B) digital line graph predicted distribution of American dipper; (C) predicted regional distribution of river otter; and (D) digital line graph predicted distribution of river otter.

plemented these by locating and mapping wetlands listed by the Environmental Protection Agency, the Idaho Department of Fish and Game, and, when available, data from the U.S. Fish and Wildlife Service's National Wetland Inventory.

The riparian buffers and wetlands were overlayed with the county and vegetation map layers. We used the county-of-occurrence and vegetation model described earlier to delineate the general distribution of riparian and wetland associated vertebrates, and then predicted the species present within that range only in wetland and riparian areas.

This model provided excellent results for those vertebrates associated with any but the smallest riparian and wetland features. Thus distributions for common loons (*Gavia immer*), great blue herons (*Ardea herodias*), northern rough-winged swallows (*Stelgidopteryx serripennis*), American dipper (*Cinclus mexicanus*), and river otters (*Lutra canadensis*) were predicted more realistically (Fig. 8B, D). However, other species were underestimated because they commonly use hydrographic features too small and numerous to map at a scale of 1:100,000. Among these species are amphibians (except plethodontid salamanders), mallards (*Anas platyrhynchos*), song sparrows (*Melospiza melodia*), water shrews (*Sorex palustris*), and muskrats (*Ondatra zibethicus*). We continue to use the general county and vegetation model for these species, with the assumption that adequate riparian or wetland microhabitats occur within each vegetation polygon. This assumption is supported by Digital Line Graph hydrography depicting hydrographic features no more than several hundred meters apart.

Creating Data Layers for Rare Taxa

In the Idaho Gap Analysis, presence or absence of a species in a county was combined with information on wildlife–habitat-relationships to produce GIS range maps for the majority of the state's terrestrial vertebrate species. Although this approach to predicting distribution works well for the more common species, it tends to overestimate the distribution of rare or patchily-distributed species, whose distribution is more difficult to predict. Therefore, we used a different approach to develop distribution maps for these rarer species.

The Idaho Natural Heritage Program (NHP) has been compiling information on the status and distribution of rare plant and animal species since 1984 (Moseley and Groves 1990). The data base of the Idaho NHP contains site-specific information on the distribution of rare species in the form of latitude–longitude coordinates and township, range, and section of known records. The data base currently tracks the status of over 100 animal species. For 38 species, we developed distribution maps using the site-specific information in the Idaho NHP data base. These 2 reptiles, 25 birds, and 11 mammals (Table 5) were selected because they met 2 qualifications: (1) each species is rare or patchily distributed, and (2) although rare, its distribution is sufficiently well known to be drawn with confidence on the basis of field inventory information.

The list of species in Table 5 includes animals classified as Idaho Department of Fish and Game Species of Special Concern, U.S. Forest Service and Bureau of Land Management Sensitive Species, and Threatened and Endangered Species under the Endangered Species Act (Moseley and Groves 1990). The type of information available on the distribution of these species varies considerably by taxon. For example, the distribution of waterbird colonies is well documented by field inventories (Trost 1985). However, the distribution of other species, such as the fisher (*Martes pennanti*) and wolverine (*Gulo gulo*), has to be inferred from incidental trappings and probable sightings that represent the best available information on their occurrence (Groves 1988). Distribution of herds of mountain sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*), 2 patchily-distributed but

Table 5. List of rare or patchily-distributed species whose distribution maps were prepared manually.

Reptiles
- Longnose snake (*Rhinocheilus lecontei*)
- Western ground snake (*Sonora semiannulata*)

Birds
- American white pelican (*Pelecanus erythrorhynchos*)
- Bald eagle (*Haliaeetus leucocephalus*)
- Black tern (*Chlidonias niger*)
- Black-crowned night-heron (*Nycticorax nycticorax*)
- Black-throated sparrow (*Amphispiza bilineata*)
- Blue grosbeak (*Guiraca caerulea*)
- California gull (*Larus californicus*)
- Caspian tern (*Sterna caspia*)
- Cattle egret (*Bubulcus ibis*)
- Common loon (*Gavia immer*)
- Common tern (*Sterna hirundo*)
- Double-crested cormorant (*Phalacrocorax auritus*)
- Forster's tern (*Sterna forsteri*)
- Franklin's gull (*Larus pipixcan*)
- Great egret (*Casmerodius albus*)
- Harlequin duck (*Histrionicus histrionicus*)
- Long-billed curlew (*Numenius americanus*)
- Peregrine falcon (*Falco peregrinus*)
- Ring-billed gull (*Larus delawarensis*)
- Sharp-tailed grouse (*Tympanuchus phasianellus*)
- Snowy egret (*Egretta thula*)
- Trumpeter swan (*Cygnus buccinator*)
- Upland sandpiper (*Bartramia longicauda*)
- White-faced ibis (*Plegadis chihi*)
- Whooping crane (*Grus americana*)

Mammals
- Coast mole (*Scapanus orarius*)
- Dark kangaroo mouse (*Microdipodops megacephalus*)
- Fisher (*Martes pennanti*)
- Grizzly bear (*Ursus arctos*)
- Idaho ground squirrel (*Spermophilus brunneus*)
- Mountain sheep (*Ovis canadensis*)
- Mountain goat (*Oreamnos americanus*)
- Northern bog lemming (*Synaptomys borealis*)
- Pinyon mouse (*Peromyscus truei*)
- Rock squirrel (*Spermophilus variegatus*)
- Wolverine (*Gulo gulo*)
- Woodland caribou (*Rangifer tarandus*)

relatively common game species, was plotted from Idaho Department of Fish and Game records.

Point data (latitude–longitude coordinates for rare species) were entered into the ARC/INFO GIS. State maps at a scale of 1:500,000 were then generated by plotting latitude–longitude distributional data of the rare species. A 1:500,000 color overlay map of habitat polygons, county boundaries, and major water bodies also was produced. With the aid of this overlay and additional ecological and distributional information for each species, predicted ranges of species were drawn by hand on the 1:500,000 state maps, which were then digitized.

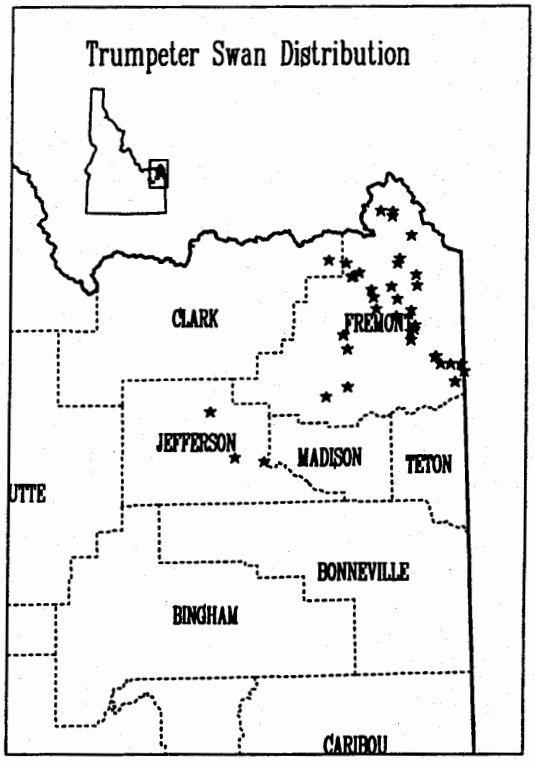

Fig. 9. Breeding territories of the trumpeter swan in Idaho known from Idaho Department of Fish and Game field surveys.

Many assumptions about the breeding distributions of species had to be made to produce range maps. Every attempt was made to combine the best site-specific distributional information with the best available ecological information. For example, the locations of trumpeter swan (*Cygnus buccinator*) nesting territories are known from extensive inventories conducted by the Idaho Department of Fish and Game (unpubl. data). Because most territories are

on small lakes and ponds and because the birds do not range far from the nest, the breeding distribution of this species is best represented by a dot distribution map (Fig. 9). As another example, the Idaho Department of Fish and Game conducted extensive inventories for harlequin ducks (*Histrionicus histrionicus*) during 1987–89 (Wallen and Groves 1988, 1989). Because harlequin ducks nest along mountain streams from which they apparently do not stray, their distribution follows stream corridors. Our predicted distribution map is a set of linear data representing stream reaches where the species is known to breed.

LAND OWNERSHIP AND MANAGEMENT STATUS DATA LAYERS

In a state-wide or region-wide Gap Analysis, land ownership categories include public (USFS, BLM, etc.) and private lands. The administering agency is important because each has different management designations and policies. In Idaho and Oregon, ownership information was taken from 1:100,000-scale Surface Management Status base maps prepared by the Bureau of Land Management. This information was useful because more than 60% of Idaho and 50% of Oregon is state or Federally owned. Because land ownership is related to the range of management possibilities, both attributes are necessary to understand the management options. If ownership data are to be useful in subsequent analyses, the data set must be kept current.

Regardless of ownership, the use and condition of any parcel of land is a result of a management decision. Private urban and agricultural lands are not managed primarily for populations of native species or for natural ecosystems, but rather for intensive human activity. Many public lands are managed primarily for resource production, although they may play a role in maintaining regional biodiversity for species and ecosystems less sensitive to disturbance (Scott et al. 1990, 1991). Wilderness areas and national parks exist because of a decision to manage primarily for natural values, including biological diversity, although they are subject to human uses that can be locally destructive of native species and natural ecosystems.

Management status refers to the degree to which an area is managed to maintain biodiversity. All land in the ownership data layer is assigned to 1 of the following 4 management status classes:

1. Management Status 1—an area with an active management plan in operation that is maintained in its natural state and within which natural disturbance events are either allowed to proceed without interference or are mimicked through management. Most national parks, Nature Conservancy preserves, some wilderness areas, Audubon Society preserves, some USFWS National Wildlife Refuges (e.g., Oregon Islands, Ash Meadows), and Research Natural Areas are included in this class.
2. Management Status 2—an area that is generally managed for its natural values, but which may receive use that degrades the quality of natural communities that are present. Most wilderness areas, USFWS Refuges managed for recreational uses, and BLM Areas of Critical Environmental Concern are included in this class.
3. Management Status 3—most nondesignated public lands, including USFS, BLM, and state park lands. Legal mandates prevent permanent conversion to anthropogenic habitat types (with some exceptions, such as tree plantations) and confer protection to populations of Federally listed endangered, threatened, and/or candidate species.
4. Management Status 4—private or public land without an existing easement or irrevocable management agreement that maintains native species and natural communities and which is managed primarily or exclusively for intensive human activity. Urban, residential and agricultural lands, public buildings and grounds, and transportation corridors are included in this class.

Often an area of high interest receives special management designation within larger managed areas (e.g., a Research Natural Area within a wilderness area within a national forest) (Fig. 10). Management may differ among areas with the same designation, however, so the degree to which an area is managed to maintain biodiversity must be assessed on an individual basis.

The design and acquisition or designation of biodiversity management areas—the implementation phase of Gap Analysis—involve topics beyond the scope of this monograph. The optimal size and shape of reserves; corridors and other avenues of connectivity; buffer zones; and management to mimic natural disturbance regimes (Noss and Harris 1986, Noss 1987*a*) are among the topics to be explored in subsequent papers related to implementation of Gap Analysis in specific settings.

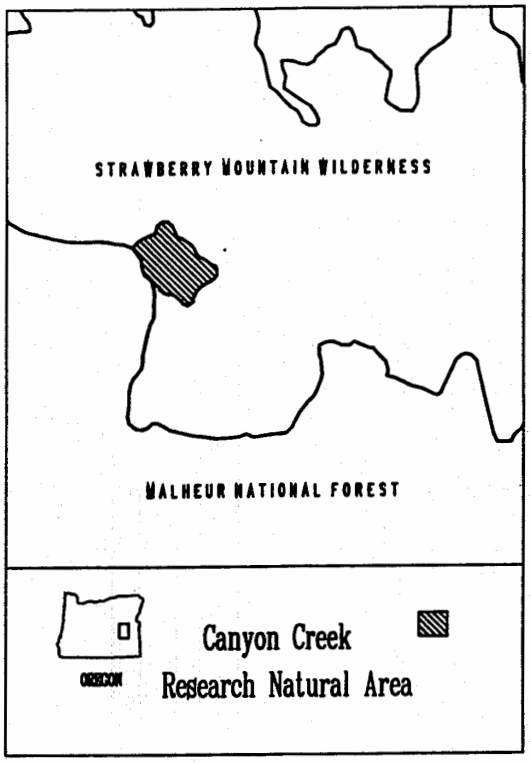

Fig. 10. A "nested" managed area: the Canyon Creek Research Natural Area within the Strawberry Mountain Wilderness Area within the Malheur National Forest, Oregon.

REGIONALIZATION

Political boundaries rarely coincide with biogeographic boundaries. Biological inventories and analyses confined to political units tend to give incomplete or biased results. For example, some species are common over large areas but are rare in a particular state. These peripheral species are the subject of much scientific curiosity, and the older literature is filled with papers with titles in the general format of "First Record of Species X from State Y." Many state conservation programs emphasize protecting populations of species or communities that are at the edge of their range and, therefore, rare in that state. Although such populations often are of evolutionary significance, perhaps more often their existence in peripheral areas is naturally tenuous or temporary. Thus, strategies to manage for the long-term maintenance of biodiversity may be better focused on the characteristic biota of a region (Noss 1983). On the other hand, peripheral populations and their habitats may assume increased importance with climate change (Hunter 1991, Quinn and Karr 1992). In any case, identifying biodiversity management areas requires an analysis of the distribution of biodiversity from the perspective of ecoregions or bioregions rather than political units.

Because the amount of land that can be managed primarily for the maintenance of biodiversity is not likely to be more than a small percentage of the land base (although conservationists will legitimately push for more), it is important that those areas selected achieve this goal with maximum efficiency. Although multiple representation of ecosystem types and species in biodiversity management areas is a good hedge against local catastrophes, it also is important to insure that all species and natural community types are represented in such areas at least once. For example, many U.S. Forest Service wilderness areas are located at higher elevations. These provide excellent and repeated opportunities to maintain alpine species and communities. Other, lower-elevation forest ecosys-

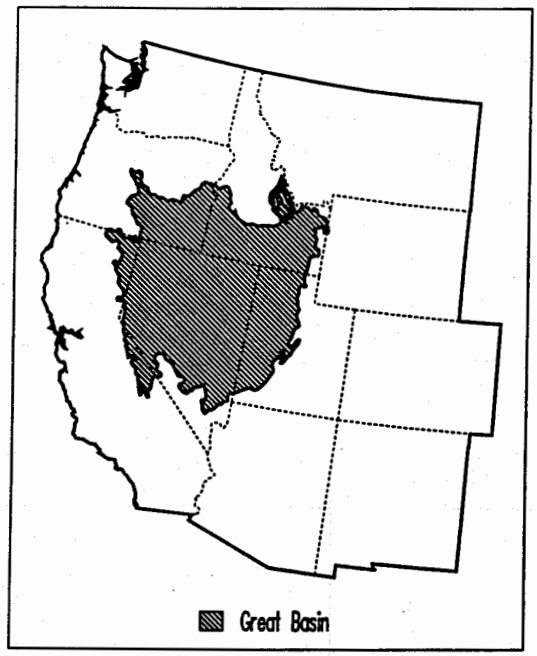

Fig. 11. Limits of the Great Basin biogeographic region, which extends into the states of Nevada, Utah, Idaho, Oregon, Wyoming, and California (adapted from Omernik 1987).

tem types (usually the most productive and diverse in species) are underrepresented in wilderness areas and other biodiversity management areas (Harris 1984).

A final argument for combining state-level biodiversity data bases into a regional or national system is the need to quantify the contribution of potential new biodiversity management areas toward the goal of maintaining national and ultimately global biodiversity. Because most species and natural community types occur in more than 1 state, state-by-state analyses cannot alone address this problem. Entire regions should be analyzed to identify areas that contain vegetation types and species not already represented in existing biodiversity management areas and to thereby set priorities for establishing additional areas managed primarily for biodiversity values.

The Great Basin division of the Intermountain faunal area, for example, overlaps the state borders of California, Oregon, Idaho, Utah, Wyoming, and Nevada (Fig. 11). The majority of the region occurs in Nevada, with a substantial fraction in Utah. If we were to analyze the distribution of species generally considered as characteristic of the region, such as the desert-adapted rodent family Heteromyidae, most of their ranges would be found in Nevada and western Utah, with peripheral populations in surrounding states. For example, there is but a single occurrence of the dark kangaroo mouse (*Microdipodops megacephalus*) in Idaho (Hafner 1985). Central Nevada or western Utah would appear to be the most efficient locations to establish reserves for Great Basin species and ecosystems. Variants of Great Basin ecosystems and species, however, must be protected in surrounding states to satisfy the legitimate conservation goals of maintaining representative ecosystems throughout their range of variation and preserving unique genetic material restricted to peripheral populations of native species (Quinn and Karr 1992).

SUMMARY

Gap Analysis is a method of identifying gaps in the protection of biodiversity at state-wide, regional, national, and, ultimately, international scales. This paper has presented the rationale and general methodology of Gap Analysis; future papers will present results for individual states and regions. The usefulness of Gap Analysis data is not restricted to identification of gaps in networks of management areas designed to maintain biodiversity. These data, and the GIS framework in which they are stored, also can serve as the basis for monitoring and evaluating changes in biodiversity at both fine and coarse scales. Some applications will require incorporation of additional GIS layers, whereas others can make use of existing layers. Some important applications include documentation of temporal and spatial change in abundance and distribution of vegetation cover types and assessment of impacts of specific "stressors" (such as air pollution or urban development) on biodiversity (Noss 1990).

Many questions in biogeography, con-

servation biology, and land-use planning can be addressed by use of Gap Analysis data. Interesting conservation questions include the following:

1. Do spatial correlations exist between areas of high species richness for various taxonomic groups?
2. Do centers of species richness correspond to centers of endemism and areas with concentrations of species that are listed as threatened, endangered, or are otherwise of special concern?
3. Can biodiversity as a whole be protected by focusing on a limited set of indicator species and cover types?
4. Can landscape linkages (broad habitat corridors) between areas of high biodiversity be identified and delineated from satellite imagery?

The potential for multiple uses of GIS-based data emphasizes the need for cooperative approaches to data acquisition and management among agencies and researchers. Using GIS, a series of discrete ecological models and spatial data bases can be linked to develop detailed pictures of how ecosystems might perform under a variety of human-induced perturbations. Although the accuracy of such models will always be limited, they provide for consideration of options to reduce and mitigate impacts for biodiversity and the environment in general.

We reiterate that Gap Analysis, as a coarse-filter approach to conservation evaluation, is not a panacea for conservation planners. Limitations must be recognized, so that additional studies can be implemented to supplement Gap Analyses. Among the limitations are the following:

1. Vegetation maps do not show habitats smaller than the minimum mapping unit. Thus, many important microhabitat elements, such as meadows and wetlands in a forest matrix, are missed. Such habitat inclusions must be captured in a subsequent, higher-resolution assessment of potential high-priority biodiversity management areas or assigned as polygon attributes without spatial coordinates.
2. Vegetation maps do not portray stand age, except for the early successional stages (herb and shrub stages) of forests following clearcutting or stand-replacing fires. Gap Analysis can identify large areas of relatively unfragmented natural forest, but is not designed to indicate how much of that forest is old growth.
3. Boundaries between vegetation types along real environmental gradients are seldom as sharp as implied by Gap Analysis vegetation maps. Ecotones and subtle gradients must be identified by higher-resolution, landscape-scale analysis.
4. Species distribution maps are predictions only. Such maps, and subsequent species richness maps, are based on known distributional limits and known or inferred habitat relationships. Although comparisons of species lists from Gap Analysis data with those from well-studied field sites have shown reasonable accuracy of predictions (70% or better, as reported above), presence of species of particular interest (such as rare ones) should be confirmed in the field prior to site-specific management activity.
5. Maps of predicted habitat distribution do not reflect habitat quality or population density. Gap Analysis predicts the presence or absence of a species, not whether it is rare or common in a particular area. Again, site-specific inventories are needed to provide abundance information.
6. Gap Analysis is not a substitute for threatened and endangered species listing and recovery efforts. A primary argument in favor of Gap Analysis is that it is proactive: it seeks to recognize and manage sites of high biodiversity value for the long-term maintenance of populations of native species and natural ecosystems before individual species and plant communities become critically rare. Thus, it should help to reduce the rate at which spe-

cies require listing as threatened or endangered. Those species that are already greatly imperiled, however, still require individual efforts to assure their recovery.

7. Gap Analysis is not a substitute for a thorough national biological inventory. As a response to rapid habitat loss, Gap Analysis provides a quick assessment of the distribution of vegetation and associated species before they are lost and provides focus and direction for a national program to maintain biodiversity. The process of improving knowledge in systematics, taxonomy, and species distributions is lengthy and expensive. That process must be continued and expedited, however, in order to provide the detailed information needed for a comprehensive assessment of our nation's biodiversity. Vegetation and species distribution maps developed for Gap Analysis can be used to make such surveys more cost effective by stratifying sampling areas according to expected variation in biological attributes.
8. Beyond inventories, further research is needed to provide better knowledge of factors influencing population viability, differences between source and sink habitats, interrelationships between species, disturbance regimes, and many other problems in ecology and conservation biology. Results from this research are needed to direct the boundary designation and management of biodiversity management areas.
9. Gap Analysis and other conservation evaluations represent a first step in a comprehensive land conservation planning program for any region. They provide base-line knowledge of the amount and distribution of several components of biological diversity and of the relationship of those components to one another in the landscape. This knowledge will be of little value if it is not applied to the land-use planning process.
10. Gap Analysis relies on remote sensing of vegetation and the relationships of animal species to vegetation types to predict the distribution and current protection status of biodiversity. We cannot overemphasize the need for field investigation before management changes are made or biodiversity management areas are established. Field studies of high priority areas should not only confirm the biodiversity values of the area, but should apply current concepts of conservation biology (such as population viability analysis, risk analysis, patch dynamics, and landscape linkages) to the delineation of management unit boundaries and the development of management plans.

We introduced this paper with the observation that saving endangered species, however laudable, fails to address the primary factors driving species toward extinction: continuing loss, fragmentation, and degradation of natural landscapes. Ideally, we envision a national and global land-use planning process that will identify and maintain much of biodiversity in a set of core biodiversity management areas (Noss 1987*b*). Sustainable human uses would take place in other wildlands that serve to both buffer and link core biodiversity management areas (Scott et al. 1990). These multiple-use wildlands are critical to the survival of mobile species with large home ranges (Brussard 1991) and will sustain metapopulations of many native plant and animal species that are less sensitive to human activities. Intensive human activities would be confined to urban, industrial, and agricultural islands in a sea of natural landscapes (Csuti 1991).

Land-use planning is a spatial exercise. If the vision of long-term maintenance of biodiversity is ever to be realized, a knowledge of the distribution and spatial relationships of the elements of biodiversity is critical. Gap Analysis develops this knowledge and applies it to a conservation evaluation that identifies a set of areas in which the elements of biodiversity are represented most efficiently. Private organiza-

tions and public agencies with an interest in maintaining biodiversity can use these results to acquire new biodiversity management areas or to change management prescriptions to emphasize the maintenance of biodiversity. In view of the value of biological support services to our society (Ehrlich and Mooney 1983) and the social and economic costs of endangered species recovery, avoiding the creation of endangered species by maintaining biodiversity in natural landscapes will serve both the conservation and development communities. The accelerating loss of many types of natural ecosystems lends urgency to a pre-emptive conservation evaluation and planning process. As long as the limitations of the Gap Analysis process are recognized, it provides a quick and efficient framework for land-use planning that will allow our species to prosper in the continuing company of our fellow citizens of the biotic community.

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