# Macroecology, Paleoecology, and Ecological Integrity of Terrestrial Species and Communities of the Interior Columbia Basin and Northern Portions of the Klamath and Great Basins

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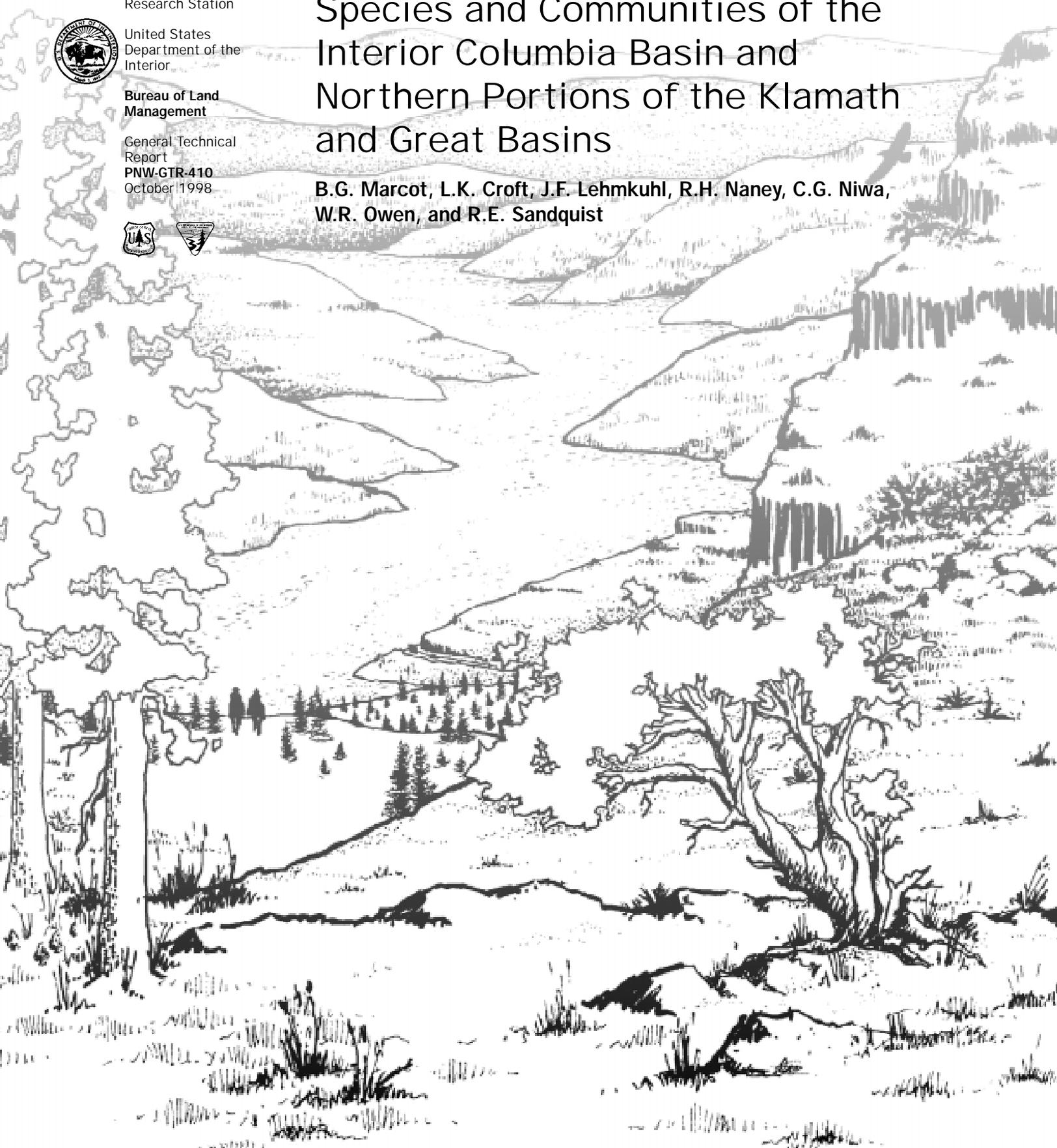
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Interior Columbia Basin Ecosystem Management Project: Scientific Assessment

Thomas M. Quigley, Editor

Abstract

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This report presents information on biogeography and broad-scale ecology (macroecology) of selected fungi, lichens, bryophytes, vascular plants, invertebrates, and vertebrates of the interior Columbia River basin and adjacent areas. Rare plants include many endemics associated with local conditions. Potential plant and invertebrate bioindicators are identified. Species ecological functions differ among communities and variously affect ecosystem diversity and productivity. Species of alpine and subalpine communities are identified that may be at risk from climate change. Maps of terrestrial ecological integrity are presented.

Keywords: Macroecology, paleoecology, ecological integrity, terrestrial communities, ecosystems, wildlife, fungi, lichens, bryophytes, vascular plants, invertebrates, arthropods, mollusks, amphibians, reptiles, birds, mammals, endemism, interior Columbia River basin, Klamath Basin, Great Basin.

Preface

The Interior Columbia Basin Ecosystem Management Project was initiated by the Forest Service and the Bureau of Land Management to respond to several critical issues including, but not limited to, forest and rangeland health, anadromous fish concerns, terrestrial species viability concerns, and the recent decline in traditional commodity flows. The charter given to the project was to develop a scientifically sound, ecosystem-based strategy for managing the lands of the interior Columbia River basin administered by the Forest Service and the Bureau of Land Management. The Science Integration Team was organized to develop a framework for ecosystem management, and assessment of the socioeconomic and biophysical systems in the basin, and an evaluation of alternative management strategies. This paper is one in a series of papers developed as background material for the framework, assessment, or evaluation of alternatives. It provides more detail than was possible to disclose directly in the primary documents.

The Science Integration Team, although organized functionally, worked hard at integrating the approaches, analyses, and conclusions. It is the collective effort of team members that provides depth and understanding to the work of the project. The Science Integration Team leadership included deputy team leaders Russel Graham and Sylvia Arbelbide; landscape ecology—Wendel Hann, Paul Hessburg, and Mark Jensen; aquatic—Jim Sedell, Kris Lee, Danny Lee, Jack Williams, Lynn Decker; economic—Richard Haynes, Amy Horne, and Nick Reyna; social science—Jim Burchfield, Steve McCool, and Jon Bumstead; terrestrial—Bruce Marcot, Kurt Nelson, John Lehmkuhl, Richard Holthausen, and Randy Hickenbottom; spatial analysis—Becky Gravenmier, John Steffenson, and Andy Wilson.

Thomas M. Quigley
Editor

USDA	United States Department of Agriculture
Forest Service logo	Forest Service

Department of the Interior seal	United States Department of the Interior
Bureau of Land Management logo	Bureau of Land Management

INTERIOR COLUMBIA BASIN ECOSYSTEM MANAGEMENT PROJECT logo	Interior Columbia Basin Ecosystem Management Project
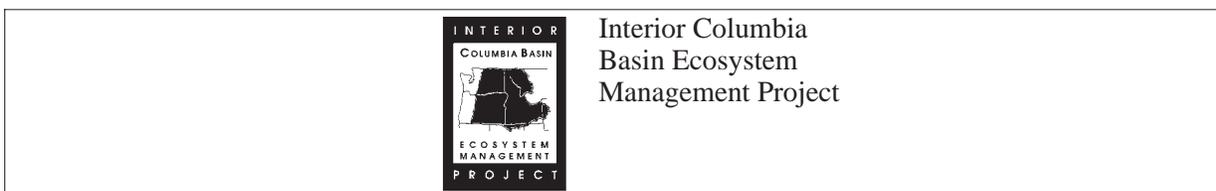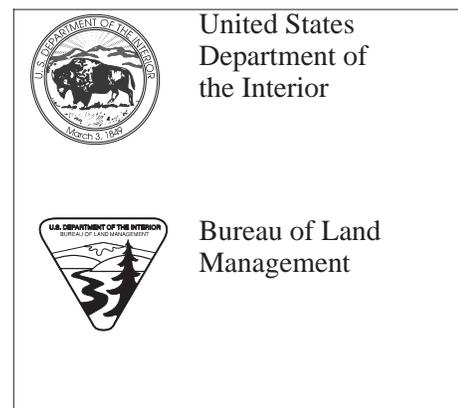
Executive Summary

Plant Biodiversity

Biodiversity of the interior Columbia River basin assessment area (hereafter referred to as the basin assessment area) is better known than is global biodiversity, but much systematic and inventory work remains to be done on soil micro-organisms, fungi, and invertebrates. Rare plants and lichen groups occur throughout the basin assessment area, and rare plants were particularly diverse in the Basin and Range, Columbia Plateau, Blue Mountains, northern Idaho, and the southern regions of the east side of the Cascade Range. Most rare plant life forms were hemicryptophytes and cryptophytes. Diversity of rare plants was not particularly oriented to specific topographic conditions, as many rare plants occur in various mostly azonal (atypical) conditions. Most rare plants are declining with fewer remaining stable; by definition, none is significantly increasing. Many paleoendemic (ancient endemic) and neoendemic (recently endemic) plants occur in the basin assessment area. Lichens disperse mostly by gravity; rare fungi by wind or vertebrates; and rare vascular plants by gravity, wind, water, and vertebrates. Most of the rare plants are pollinated probably by various invertebrates. Several lichens, bryophytes, plants, and invertebrates can serve as bioindicators of environmental conditions and ecosystem health.

Animal Biodiversity

Invertebrates of the basin assessment area disperse by many means. One way involving coevolution between invertebrates and vertebrates is phoresis (dispersal by hitching a ride on vertebrate organisms). Disease and parasites are poorly studied in the basin assessment area and need further work to determine distribution, frequency of occurrence, and effects on plants and animals of interest to management. Endemic vertebrates include some amphibians, birds, and mammals. The ranges of many vertebrate species extend beyond the basin assessment area, including semiendemics (species occurring only within the inland West or the basin assessment area for only a portion of the year, as with some migrants). Thus, to provide for their rangewide viability, conditions beyond the basin assessment area need to be known and addressed. Numbers of breeding birds by state match other published predictions. Most bird species were ranked as common, with fewer uncommon, rare, abundant, or irregular. More abundant and irregularly occurring bird species occur toward midcontinent than elsewhere in the basin assessment area. Most birds are resident or summer breeders, with fewer being migrants or wintering only in the basin assessment area.

Ecological Functions of Species Among Communities

We present species function profiles that relate key ecological functions (KEFs)—those major roles that each species plays in their environment—of vertebrates to occurrence by vegetation community. Key ecological functions of species can affect ecosystem productivity, diversity, and sustainability; and function profiles of species help summarize the diversity of species functions in ecological communities of the basin assessment area. Function profiles of species display the degree of functional redundancy (number of species sharing the same KEF) within each community. Some functions, particularly cavity excavation in snags and primary burrow excavation in soil, are highly variable among communities in terms of number of species. Late seral forests provide the greatest redundancy in carrion feeding, general nutrient cycling, and primary cavity excavation functions of vertebrates. We discuss functions and functional redundancy of other communities as well. We pose several hypotheses relating species functional redundancy to ecosystem resiliency and changes in species community structure, as one facet of ecosystem management. The greatest vertebrate functional diversity is found in early seral montane forest, followed by upland woodlands and riparian woodlands, and upland shrublands. No one community, however, contains all ecological functions of species.

Effects of Climate Change

Near-future changes in regional climates from human activities may be complex, involving increasing interseasonal and interannual variations in precipitation and temperature. Species preadapted to such variations likely will persist during climate changes. The fate of vertebrates within alpine tundra and subalpine forests may differ individualistically according to latitudinal shifts of these habitats and the range of plasticity of each species. Studies of climate change suggest that patterns of climate, vegetation, and plant and animal species occurrence in the basin assessment area during historic (since 1800) times do not match those over the past four centuries or prehistorically during the Quaternary or Tertiary periods. This has important ramifications for reinterpreting the range of natural historic conditions (variations), which do not represent conditions under which species evolved.

Prehistoric Conditions

The assemblage of mammalian taxa of the basin assessment area has changed greatly since Tertiary and Quaternary periods, in accord with changes in climate and vegetation, although overall diversity of species among families and orders has remained more or less constant. Many species, and some families and orders, have declined or become extinct, whereas others have radiated and grown. We anticipate future losses and gains in species, families, and orders of plants and animals over evolutionary time, although prehistoric trends in extinction and speciation (evolution of new species) do not represent short-term ecological conditions.

Ecological Integrity of Terrestrial Communities

We mapped various aspects of terrestrial ecological integrity, including components of species viability (as threatened, endangered and candidate species, locally endemic species, distribution of rare plants, and key habitat corridors); long-term evolutionary potential of species (as disjunct populations and biodiversity and endemism hot spots); and multiple ecological domains (as peripheral species and unique species assemblages, and the full set of large vertebrate carnivores). Results are shown by watershed.

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CHAPTER 1

Introduction

History and Impetus

The Science Integration Team of the Interior Columbia Basin Ecosystem Management Project (ICBEMP) conducted ecological assessments during 1993-96 as a joint venture among USDA Forest Service (FS), USDI Bureau of Land Management (BLM), and many cooperators. The Science Integration Team developed the first comprehensive database and assessment of terrestrial plant and animal ecology of the interior Columbia River basin and northern portions of the Klamath and Great Basins in the United States (collectively, and hereafter, referred to as the basin assessment area) (Marcot and others 1997). This document expands on findings related to macroecology and ecological integrity of terrestrial species and communities of the basin assessment area.

Our ultimate aim is to contribute to a scientific foundation for ecosystem management of terrestrial ecosystems in the basin assessment area. According to the Ecological Society of America (1995), a scientific basis for ecosystem management should provide adequate information on biological diversity and on the function and dynamics of ecosystems, and acknowledge the "openness and interconnectedness" of ecosystems.

Other facets of ecosystem management should entail study of past and current natural ranges of conditions (Morgan and others 1994) and the ecological roles of species interactions (Willson 1996). This report provides information on these topics in terrestrial ecosystems of the basin assessment area.

Definitions

In this report, **macroecology** refers to habitat and environmental characteristics of individual terrestrial species or species groups at the broad scale (sensu Brown 1995). **Terrestrial species** refers to species whose life histories are mostly confined to nonaquatic environments, although some largely aquatic vertebrate species such as amphibians and otters (but not fish) are included.

Hydrologic unit codes (HUCs), as used in the ICBEMP ecology assessments, are standard delineations of watershed and subwatershed land areas based on river drainage patterns (Jensen and Bourgeron 1994). We used two levels of HUCs: 4th- and 6th-level hydrologic units, corresponding to subbasins and subwatersheds, respectively.

Broad scale is defined here as such basin assessment area-wide depictions that use characterizations of 1-km^2 cells with summarization by 4th-code hydrologic units. **Mid scale** is defined as characterizations at 4-ha resolution with summarization by 6th-code hydrologic units.

CHAPTER 2

Study Area

Area and Boundaries

The basin assessment area encompasses 58 361 400 ha. It is confined on the north by the United States-Canada border; on the east by the Continental Divide; on the west by the crest of the Cascade Range; on the south by the Oregon-California and Oregon-Nevada borders; and elsewhere by the extent of the Columbia River drainage (fig. 1). One major portion of the Columbia River basin in the United States is the tributary Snake River basin, which includes central and southern Idaho and western Montana.
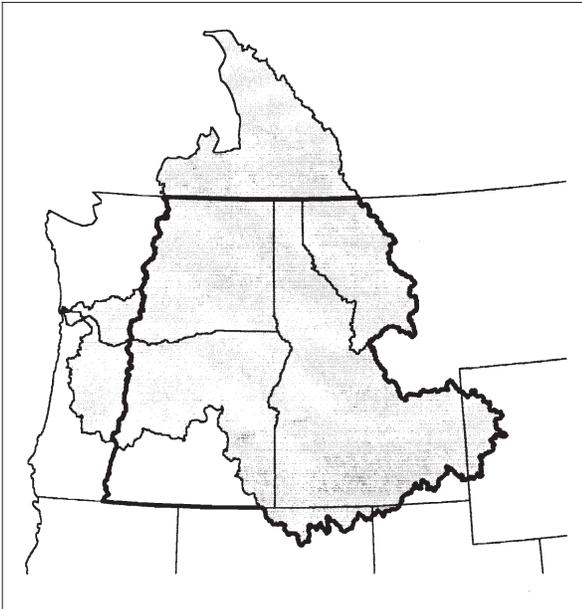

Figure 1—Boundaries of the Columbia River basin in North America (shaded area), and the basin assessment area (heavy solid line) and Western States (light solid lines) in the United States.

It extends toward the Continental Divide into the Greater Yellowstone Ecosystem and southern Yellowstone National Park. The entire Columbia River basin encompasses about 67 466 000 ha and extends north into British Columbia, Canada, (15 percent of the entire area of the Columbia River basin proper) and west past the crest of the Cascade Range to the Pacific Ocean, outside the boundaries of the basin assessment area (fig. 1).

The basin assessment area was defined by the directors of the ICBEMP according to both agency planning needs and hydrologic (watershed) criteria. The existing Northwest Forest Plan and its preceding ecological assessment (Forest Ecosystem Management Assessment Team [FEMAT] 1993) had already addressed the area within the range of the northern spotted owl, including the eastern slope of the Cascade Range. The ICBEMP was directed to reevaluate the FEMAT assessments along the east side of the Cascade Range, given the different composition of forests found there as compared to forests west of the crest of the Cascade Range.

The basin assessment area includes portions of seven Western states, including major portions of Washington, Oregon, and Idaho, as well as western Montana and corners of Wyoming, Utah, and Nevada. Although outside the Columbia River basin per se, the northern portions of the Klamath Basin (1.5 million ha of the basin assessment area) and Great Basin (4.2 million ha of the basin assessment area) in southern Oregon were included in the basin assessment area. The purpose was to complete broad-scale land planning and assessments on BLM and FS lands within the regional boundaries of these agencies in Oregon. The portions of the Klamath Basin and northern Great Basin are therefore also included in the assessments of this report, although they do not form a discrete ecological unit.

By Land Ownership

Bureau of Land Management and FS lands constitute 53 percent of the land within the basin assessment area, with the remainder in private (38 percent), State and other Federal (4 percent), tribal (4 percent), and national park and other non-Federal wilderness (1 percent) lands (fig. 2). The basin assessment area includes portions of major ecosystems of interest to Federal broad-scale planning concerns, including the Greater Yellowstone Ecosystem, the mountain ranges of the North Cascades/Bitterroots, the Selkirks, the Cabinet-Yaks, the High Cascades, the Klamath Basin, the Great Basin, and others.

By Type of Management

Most of the basin assessment area is roaded and actively managed for natural resource use (fig. 3). Of all ownerships within the basin assessment area, 81 percent of the area is roaded and actively managed (43 percent BLM-FS plus 38 percent other lands), 10 percent is unroaded or not actively managed (9 percent BLM-FS plus 1 percent National Park Service and other wilderness lands), and 10 percent is tribal, state, and other public lands of varying use, mostly roaded and actively managed. Of all BLM and FS lands within the basin assessment area, 83 percent is roaded and actively managed for natural resource use and extraction, and 17 percent is characterized as unroaded.

Ecological Reporting Units

The Science Integration Team mapped 13 ecological reporting units (ERUs) in the basin assessment area. Ecological reporting units are geographically defined areas identified by the Science Integration Team by use of multiple landscape and watershed criteria and were based on subsection delineations of 6th-code HUCs (Jensen and others, in prep.). Ecological reporting units represent large geographic areas with common landforms and drainage patterns, such as the Upper Snake headwaters, northern glaciated mountains, and the east side of the Cascade Range in Oregon.

Hydrologic Delineations and Biophysical Characterizations

The basin assessment area was partitioned into 164 subbasins or 4th-code HUCs, and 7,733 subwatersheds or 6th-code HUCs. The subbasins averaged 356 496 ha and ranged from 4700 to 1 080 500 ha. The subwatersheds averaged 7880 ha and ranged from 96 to 86 500 ha. The 4th- and 6th-code HUCs of the basin assessment area were characterized by sundry biophysical parameters, including historic and current vegetation cover types and structural stages (Hann and others 1997), historic and current terrestrial vegetation communities (Hann and others 1997), highest and lowest annual precipitation (available data from 1989), landform, highest and lowest elevation, and topographic relief.[1]

The basin assessment area also was characterized by landform. It contains nine major landforms ranging from arid grasslands and lowland plains and valleys, to intermontane basins and breaks, to steep mountains and glaciated ranges, and a wide variation in topography, precipitation, and climate patterns.

Vegetation Cover Types and Terrestrial Vegetation Communities

This section describes the vegetation classifications used in this analysis and summarizes the current and historic vegetation character of the basin assessment area as presented in various chapters in Quigley and Arbelbide (1997).

Vegetation characterizations of the basin assessment area—The current vegetation condition of the basin assessment area was characterized by use of 44 vegetation cover types (table 1) and 24 terrestrial vegetation communities (table 2) (Hann and others 1997). The vegetation communities are combinations of 41 vegetation cover types (table 3) and structural stages (see Hann and others 1997, for descriptions and methods). For some analyses, vegetation communities better represent general conditions than do their component cover types.

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[1] Biophysical data from Intermountain Fire Sciences Laboratory, USDA Forest Service, P.O. Box 8089, Missoula, MT 59807.
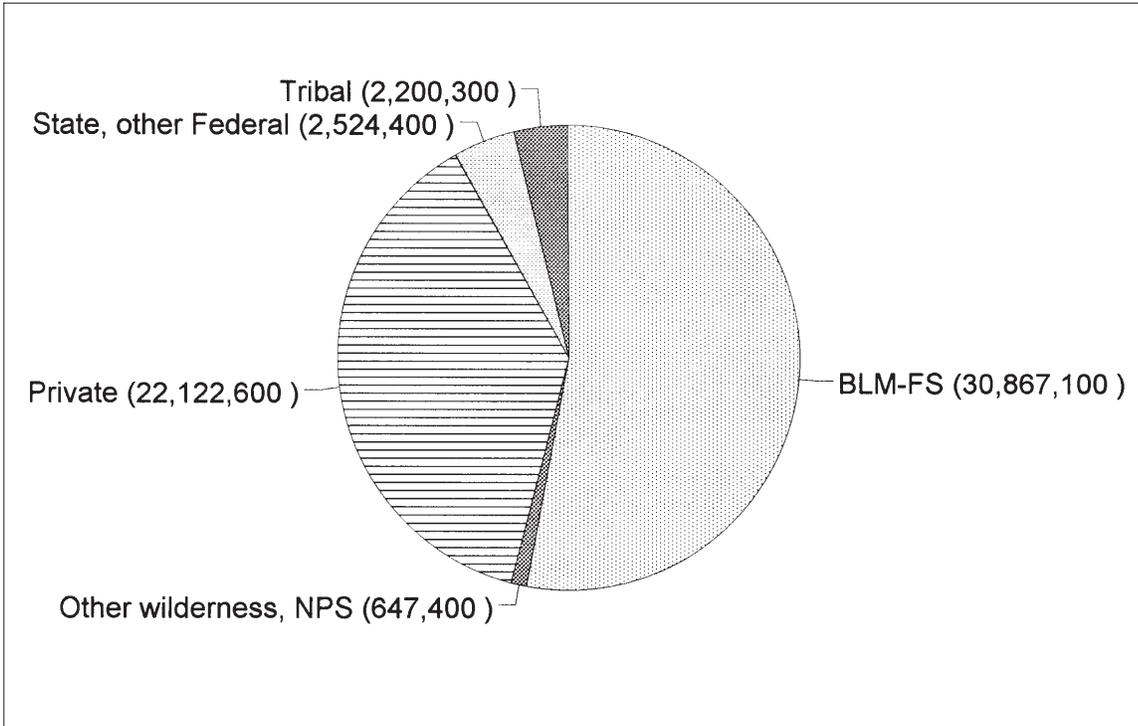
Figure 2—Distribution (hectares) of land ownership and administration in the basin assessment area (source: ICBEMP, GIS 1-km^2 raster data).
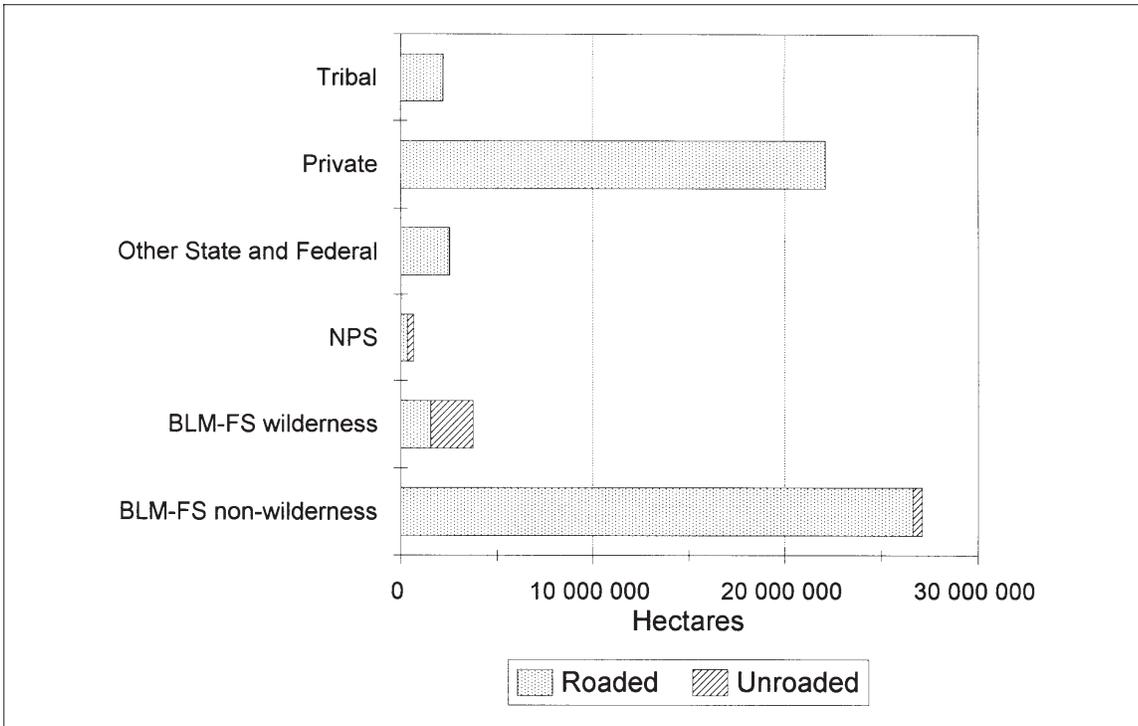

Figure 3—Distribution of land by management emphasis, and by unroaded or roaded conditions, in the basin assessment area (source: ICBEMP, GIS 1-km^2 raster data).

Table 1—Names of 44 vegetation cover types denoted for the basin assessment area[a]

Cover-type code	Vegetation cover-type name
CRB003	Shrub or herb/tree regeneration
CRB005	Alpine tundra
CRB006	Barren
CRB007	Herbaceous wetlands
CRB008	Pacific silver fir/mountain hemlock
CRBS01	Juniper woodlands
CRBS02	Mixed-conifer woodlands
CRBS03	Juniper/sagebrush
CRBS04	Big sagebrush
CRBS05	Shrub wetlands
CRBS06	*Agropyron* bunchgrass
CRBS07	Native forb
CRBS08	Exotic forbs/annual grass
CRBS09	Grand fir/white fir
CRBS10	White bark pine/alpine larch
CRBS11	Red fir
CRBS12	Cropland/hay/pasture
CRBS13	*Fescue*-bunchgrass
CRBS19	Urban
CRBS20	Water
SAF205	Mountain hemlock
SAF206	Engelmann spruce/subalpine fir
SAF208	Whitebark pine
SAF210	Interior Douglas-fir
SAF212	Western larch
SAF215	Western white pine
SAF217	Aspen
SAF218	Lodgepole pine
SAF219	Limber pine
SAF227	Western redcedar/western hemlock
SAF233	Oregon white oak
SAF235	Cottonwood/willow
SAF237	Interior ponderosa pine
SAF243	Sierra Nevada mixed conifer
SAF245	Pacific ponderosa pine
SRM104	Antelope bitterbrush/bluebunch wheatgrass
SRM322	Mountain mahogany
SRM402	Mountain big sagebrush
SRM406	Low sage
SRM414	Salt desert shrub
SRM421	Chokecherry/serviceberry/rose

[a] Source: Hann and others (1997). Only 41 cover types are listed here; 3 additional cover types were dropped from the overall list after initial analyses were conducted for this report. The dropped cover types were either extremely rare or found to not occur in the basin assessment area after subsequent study.

Table 2—Names and abbreviations of 24 terrestrial vegetation communities denoted for the basin assessment area[a]

Abbreviation	Terrestrial vegetation community name
AGRICUL	Agricultural
ALPINE	Alpine
EXOTICS	Exotics
MIXCONES	Early seral montane forest
MIXCONLM	Late seral montane multilayer
MIXCONLS	Late seral montane single layer
MIXCONMS	Mid seral montane forest
NFHERBUP	Upland herb
NFUPSHRB	Upland shrub
PINFORES	Early seral ponderosa pine forest
PINFORLM	Late seral ponderosa pine forest multilayer
PINFORLS	Late seral ponderosa pine forest single layer
PINFORMS	Mid seral ponderosa pine forest
RIPHERB	Riparian herb
RIPSHRUB	Riparian shrub
RIPWDLND	Riparian woodland
ROCK	Rock/barren
SUBFUPES	Early seral subalpine forest
SUBFUPLM	Late seral subalpine forest multilayer
SUBFUPLS	Late seral subalpine forest single layer
SUBFUPMS	Mid seral subalpine forest
URBAN	Urban
WATER	Water
WOODLDUP	Woodland upland

[a] Source: Hann and others 1997.

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Table 3—Crosswalk between terrestrial vegetation communities and vegetation cover types[a]

Terrestrial vegetation community abbreviation	Vegetation cover-type code
AGRICUL	CRBS12
ALPINE	CRB005
EXOTICS	CRBS08
MIXCONES	CRB003
MIXCONES	CRB008
MIXCONES	CRBS09
MIXCONES	CRBS11
MIXCONES	SAF210
MIXCONES	SAF212
MIXCONES	SAF215
MIXCONES	SAF218
MIXCONES	SAF227
MIXCONES	SAF243
MIXCONLM	CRB008
MIXCONLM	CRBS09
MIXCONLM	CRBS11
MIXCONLM	SAF210
MIXCONLM	SAF212
MIXCONLM	SAF215
MIXCONLM	SAF218
MIXCONLM	SAF227
MIXCONLM	SAF243
MIXCONLS	CRBS09
MIXCONLS	SAF210
MIXCONLS	SAF212
MIXCONLS	SAF215
MIXCONLS	SAF218
MIXCONLS	SAF227
MIXCONLS	SAF243
MIXCONMS	CRB008
MIXCONMS	CRBS09
MIXCONMS	CRBS11
MIXCONMS	SAF210
MIXCONMS	SAF212
MIXCONMS	SAF215
MIXCONMS	SAF218
MIXCONMS	SAF227
MIXCONMS	SAF243
NFHERBUP	CRBS06
NFHERBUP	CRBS07
NFHERBUP	CRBS13
NFUPSHRB	CRBS04
NFUPSHRB	SRM104
NFUPSHRB	SRM322
NFUPSHRB	SRM402
NFUPSHRB	SRM406

Table 3—Crosswalk between terrestrial vegetation communities and vegetation cover types[a] (continued)

Terrestrial vegetation community abbreviation	Vegetation cover-type code
NFUPSHRB	SRM414
NFUPSHRB	SRM421
PINFORES	SAF237
PINFORES	SAF245
PINFORLM	SAF237
PINFORLM	SAF245
PINFORLS	SAF237
PINFORLS	SAF245
PINFORMS	SAF237
PINFORMS	SAF245
RIPHERB	CRB007
RIPSHRUB	CRBS05
RIPWDLND	SAF217
RIPWDLND	SAF235
ROCK	CRB006
SUBFUPES	CRBS10
SUBFUPES	SAF205
SUBFUPES	SAF206
SUBFUPES	SAF208
SUBFUPLM	CRBS10
SUBFUPLM	SAF205
SUBFUPLM	SAF206
SUBFUPLM	SAF208
SUBFUPLS	SAF205
SUBFUPLS	SAF208
SUBFUPMS	CRBS10
SUBFUPMS	SAF205
SUBFUPMS	SAF206
SUBFUPMS	SAF208
URBAN	CRBS19
WATER	CRBS20
WOODLDUP	CRBS01
WOODLDUP	CRBS02
WOODLDUP	CRBS03
WOODLDUP	SAF219
WOODLDUP	SAF233

[a] Terrestrial vegetation communities are a combination of vegetation cover types and structural stages (not shown here). See table 2 for the terrestrial vegetation community names associated with the vegetation community abbreviations and table 1 for vegetation cover-type names associated with the cover-type codes.

Present vegetation conditions—At present, the five most dominant vegetation cover types of the basin assessment area (all lands and ownerships) are big sagebrush (16 percent of the assessment area), cropland-hayland-pasture (16 percent), interior ponderosa pine (*Pinus ponderosa*)[2] forest (10 percent), interior Douglas-fir (*Pseudotsuga menziesii*) (8 percent), and lodgepole pine (*Pinus contorta*) forest (7 percent). The cropland-hayland-pasture has been carved mostly from native grassland types.

Terrestrial vegetation communities are a combination of cover type and structural stage. As such, the terrestrial vegetation communities show similar patterns of dominance as those of vegetation cover types and structural stages, but additionally help reveal differences among some of the general seral forest conditions. The five most dominant terrestrial vegetation communities of the basin assessment area (all lands and ownerships) at present are upland shrub (26 percent of the assessment area), mid seral montane forest (17 percent), agricultural (16 percent), early seral montane forest (8 percent), and mid seral ponderosa pine forest (8 percent) (fig. 4).

Change since historic conditions—Hann and others (1997) present data on change of vegetation cover types and terrestrial vegetation communities since early historic times (about early 1800s). The vegetation cover types having undergone the greatest historic decline in percentage of original area occupied in the basin assessment area (that is, less than -50 percent change from historic area), are western white pine (*Pinus monticola)* forest (-96 percent change), whitebark pine (*Pinus albicaulis*)/subalpine larch (*Larix lyallii*) forest (-95 percent), native forb (-92 percent), *Agropyron* bunchgrass (-68 percent),

Fescue bunchgrass (-66 percent), cottonwood (*Populus* spp.)/willow (*Salix* spp.) (-64 percent), and shrub wetlands (-61 percent).[3] The vegetation cover types having undergone the greatest historic increases (that is, > +50 percent change from historic area) are mountain hemlock (*Tsuga mertensiana*) forest (53 percent), Pacific ponderosa pine (80 percent), juniper (*Juniperus* spp.)/ sagebrush (*Artemesia* spp.) (163 percent), mountain mahogany (*Cercocarpus ledifolius*) (406 percent), western redcedar (*Thuja plicata*) western hemlock (*Tsuga heterophylla*) (853 percent), grand fir (*Abies grandis*) white fir (*Abies concolor*) (965 percent), and Pacific silver fir (*Abies amabilis*) mountain hemlock (1,733 percent). Many of the increases in these forest types have resulted from selective high-grade logging (for example, of old-growth ponderosa pine trees) and fire-suppression activities, resulting in major changes in tree dominance and stand structure (see Hann and others [1997], for data on absolute changes of each cover type).

The terrestrial vegetation communities decreasing the most since historic time (that is, less than -50 percent) (fig. 5) include late seral lower montane (including ponderosa pine) single-layer forest (-81 percent change), early seral lower montane forest (-77 percent), upland herb (-67 percent), and late seral subalpine multilayer forest (-64 percent). Terrestrial vegetation communities most increasing since historic time (that is, greater than 50 percent) include mid seral lower montane forest (53 percent) and mid seral montane forest (59 percent). Urban areas, exotic communities, and agricultural areas also have greatly increased, as they were virtually absent under early historic conditions. They were carved mostly from native upland grassland, herbland, and shrubland communities (fig. 6; see Hann and others [1997] for definitions of urban, exotic, and agricultural communities). Changes in rangeland communities have been due to increased fire frequency associated with the invasion of exotic grasses, primarily cheatgrass (*Bromus tectorum*).

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[2] Authorities for species can be found in the following references: mosses and nonvascular plants, Schofield (1980) and Vitt and others (1988); plants and allies, Hitchcock and others (1969); invertebrates, Furniss and Carolin (1980); amphibians and reptiles, Collins (1990); birds, AOU (1983 with supplements); mammals, Jones and others (1992) and Wilson and Reeder (1993).

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[3] In addition, Sierra Nevada mixed-conifer forest has undergone significant decline, although this cover type may have been identified as an artifact within the basin assessment areas and is not included here in the analyses.
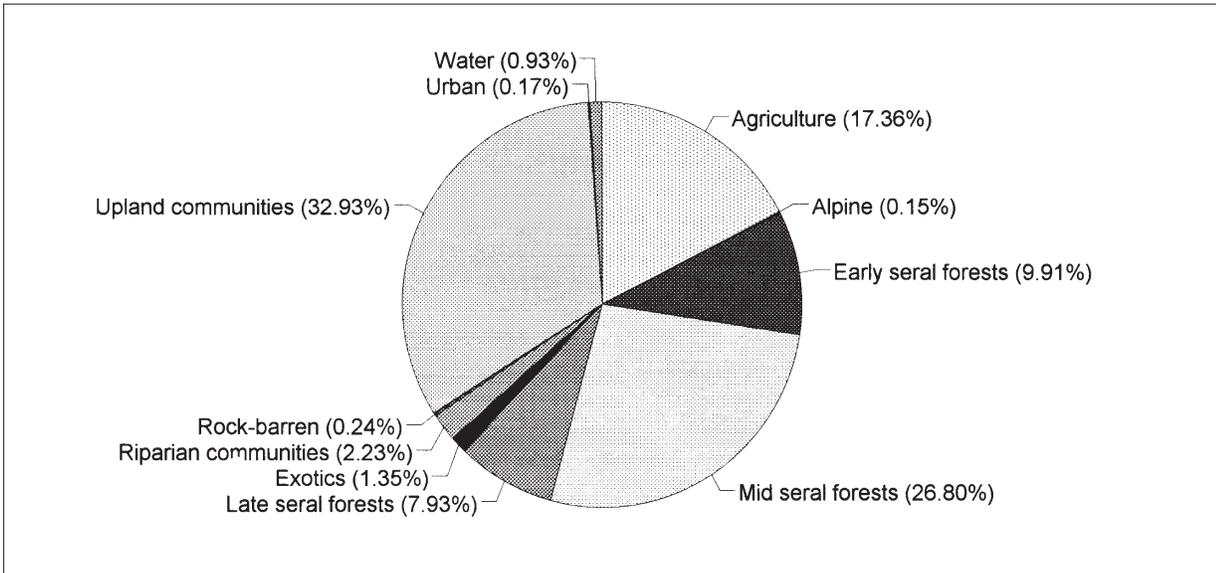
Figure 4—Current distribution of terrestrial vegetation communities in the basin assessment area (source: ICBEMP, GIS 1-km^2 raster data).
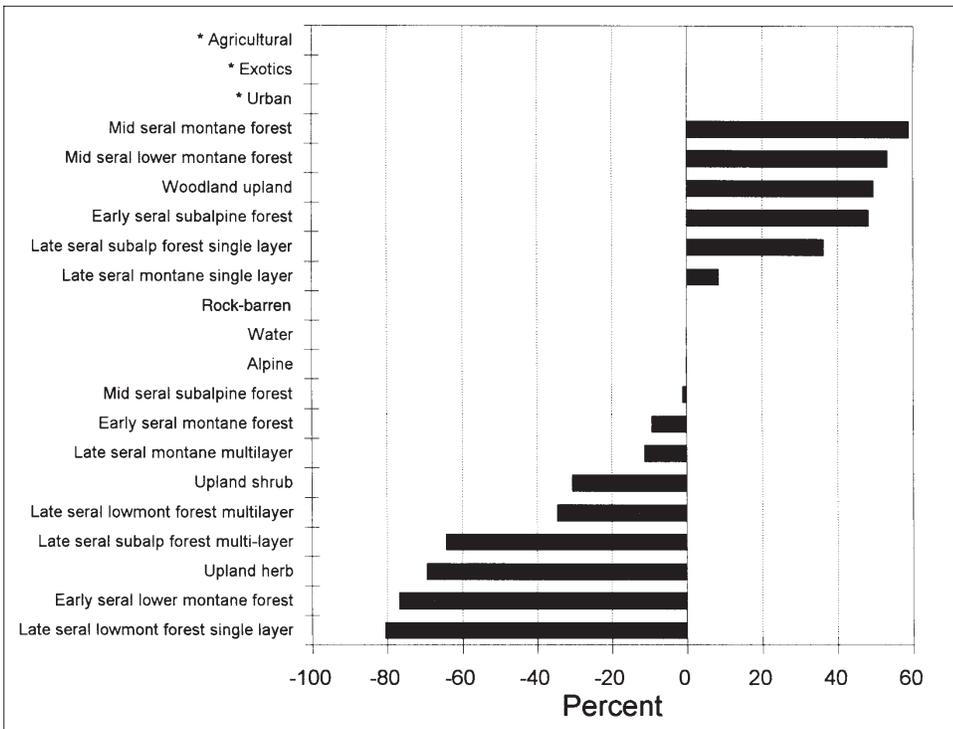

Figure 5—Percentage of changes of area covered by terrestrial vegetation communities from historic (early 1800s) to current time, in the basin assessment area: * = not historically present, lowmont = lower montane, subalp = subalpine (source: ICBEMP, GIS 1-km^2 raster data).

10

35 000 000

30 000 000

25 000 000

20 000 000

Hectares

15 000 000

10 000 000

5 000 000

0

Historic   Current

Exotics

Upland shrub

Upland herb

Woodland upland
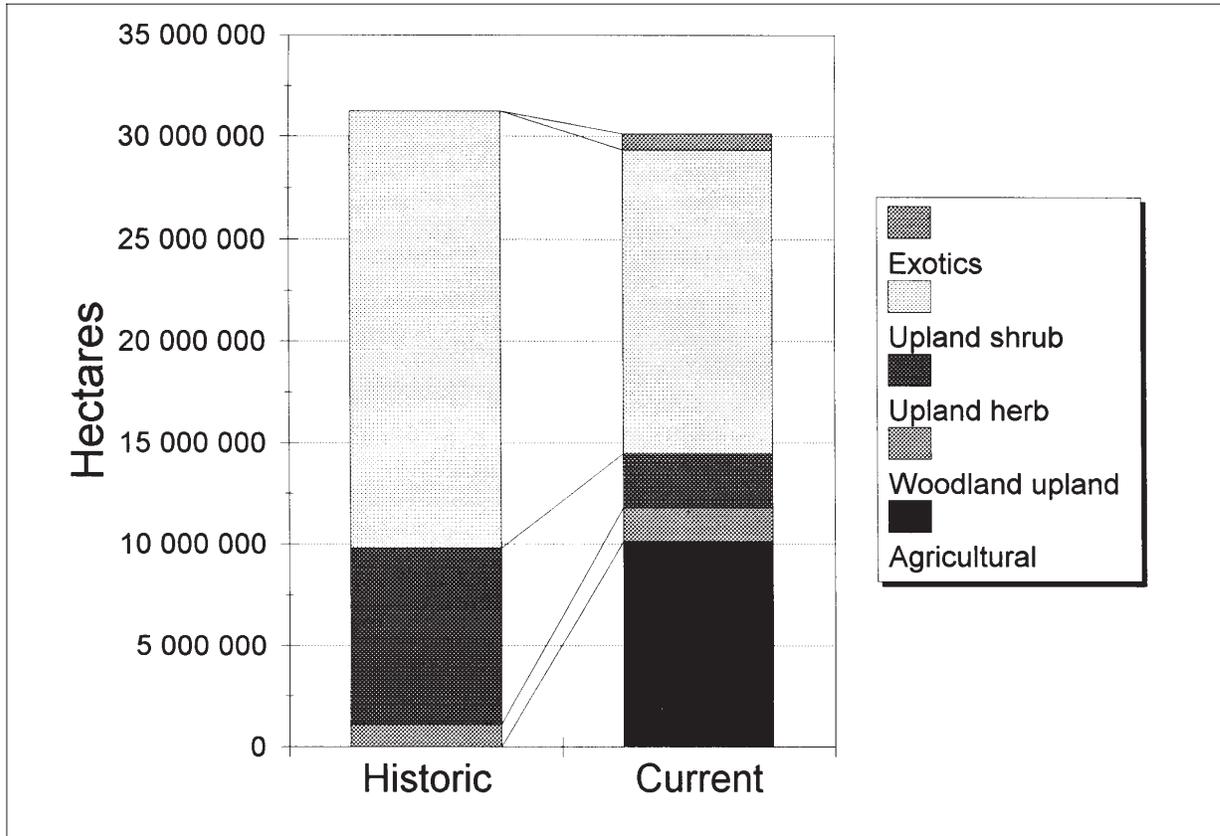
Agricultural

Figure 6—Historic (early 1800s) and current area of nonforest vegetation communities of the basin assessment area, showing increase in areas of agricultural and exotic vegetation (source: ICBEMP, GIS 1-km^2 raster data).

Combining terrestrial vegetation communities of similar seral conditions but different forest types simplifies the picture (fig. 7). The greatest historic declines have occurred in late seral forests (-44 percent) and native upland types (including native grasslands and shrublands, collectively -38 percent). The greatest historic increases have occurred in mid seral forests (48 percent) as well as urban, exotics, and agricultural communities.

Since historic times, there has been a slight increase in overall forest cover (fig. 8) because fire suppression has encouraged expansion of juniper woodland and interior Douglas-fir forest into native sagebrush and grassland communities. Of all forest communities combined, early seral forests have declined slightly, mid seral forests increased by about half again, and late seral forests have decreased by half of their original area (fig. 8). Separating out these seral stages, we can see how

forest types have differentially changed (fig. 9). Of the slight overall decline in area of early seral forests, ponderosa pine forest has declined the greatest, montane forest has declined somewhat, and subalpine forest has increased in area (fig. 9a). Of the overall increase in area of mid seral forests, montane forest and ponderosa pine forest have greatly increased, while subalpine forest has remained relatively constant in area (fig. 9b). Of the overall sharp decline in area of late seral forests, ponderosa pine single-layer forest and subalpine forest multilayer forest have had the greatest declines; ponderosa pine multilayer forest and montane multilayer forest have declined somewhat less; and montane single-layer forest and subalpine single-layer forest have slightly increased (fig. 9c). We will see later that these changes have ramifications for associated plant and animal species.

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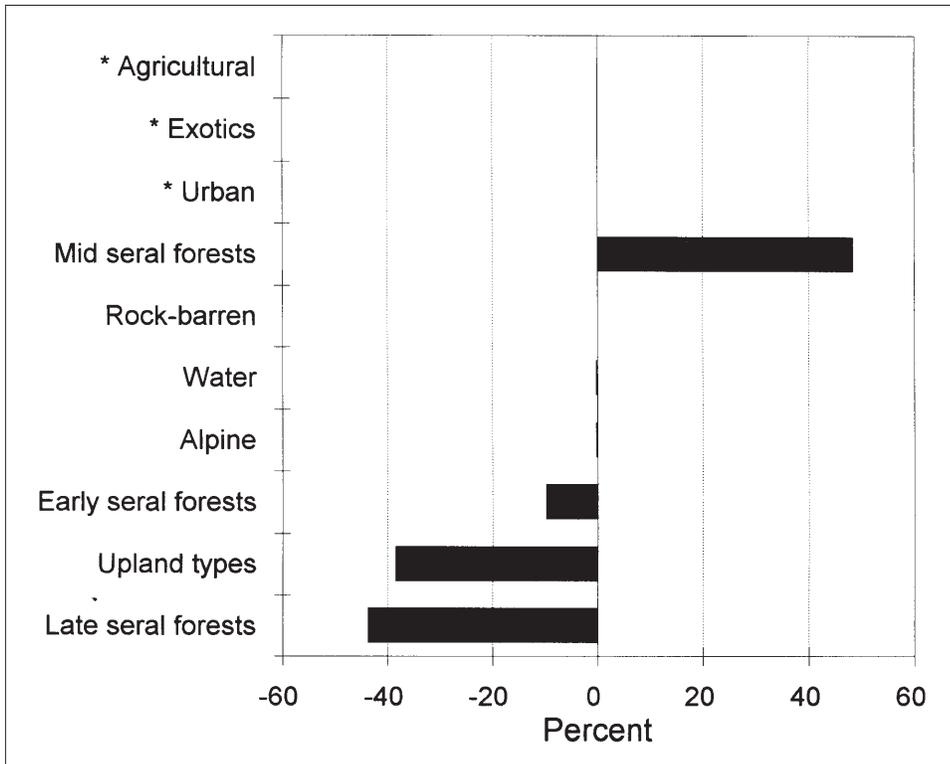
Figure 7—Percentage of changes of area covered by terrestrial vegetation communities, combined into seral stage categories, from historic (early 1800s) to current time, in the basin assessment area: * = not historically present (source: ICBEMP, GIS 1-km^2 raster data).
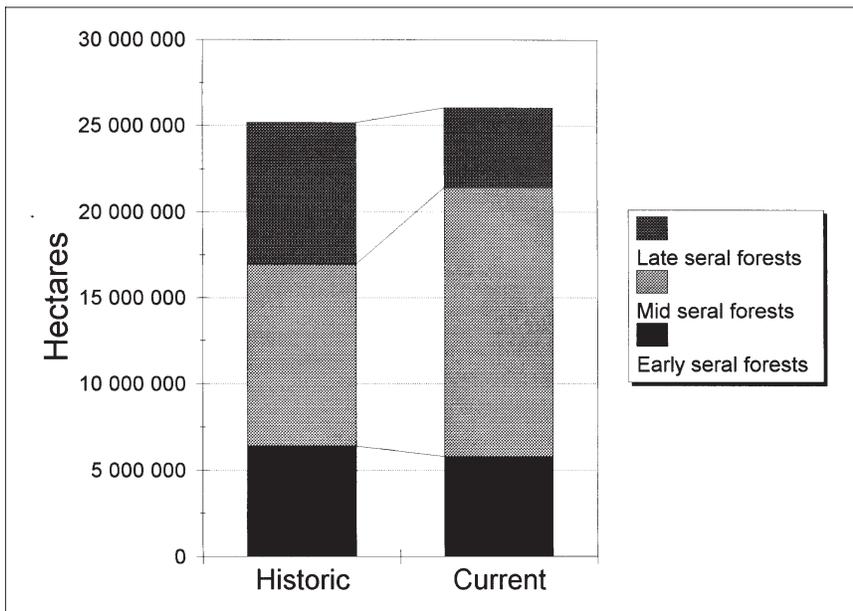

Figure 8—Historic (early 1800s) and current area of forest vegetation communities combined by seral stage, in the basin assessment area (source: ICBEMP, GIS 1-km^2 raster data).
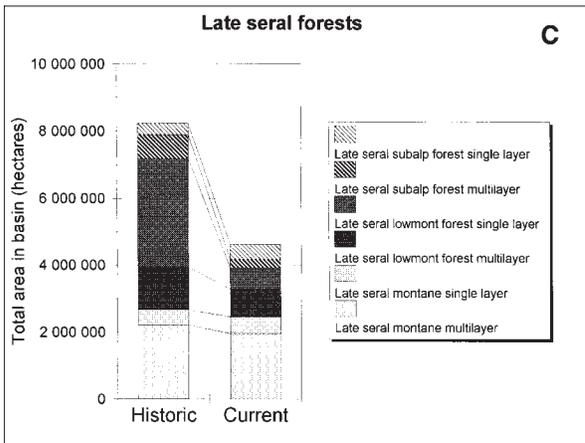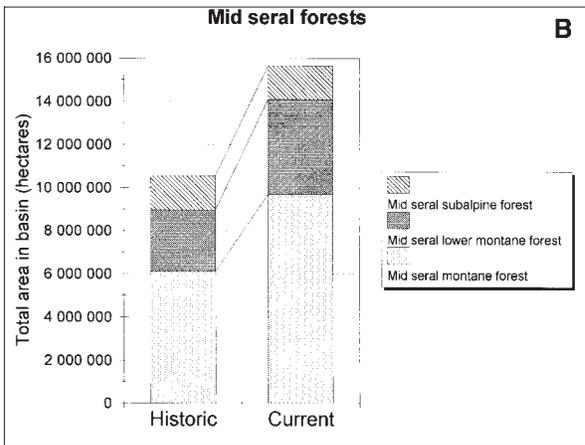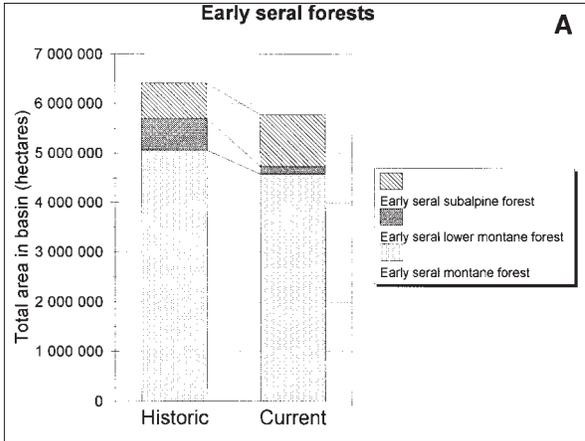
Figure 9—Historic (early 1800s) and current area of individual forest vegetation communities by (A) early, (B) mid, and (C) late seral stage, in the basin assessment area; lowmont = lower montane, subalp = subalpine (source: ICBEMP, GIS 1-km^2 raster data).

Chapter 3

Methods

Geographic Area Estimates

Estimates of geographic areas are from ArcInfo®[1] geographic information systems (GIS) 1-km^2 raster data, provided by the ICBEMP.

Species Data Collection

Data on species distribution and ecology were gathered from literature and panels of species experts. Methods for data collection and lists of experts consulted were presented in Marcot and others (in prep.).

Further Explorations of Terrestrial Biodiversity

Global patterns of species richness (number of species) by taxonomic class were compared with those of the basin assessment area to determine differences or similarities. Global richness values were tallied from the literature, which presented number of known species and low and high estimated values. Values of species richness from the basin assessment area were tallied as single values
for number of known species and number of estimated species (Marcot and others 1997). The poorest known taxonomic classes are those with the lowest proportion of estimated species that have been scientifically verified from the assessment area. These were compared with global patterns. Implications of terrestrial biodiversity patterns for management are identified based on similarities of these patterns.

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[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Assessment of Macroecology of Individual Species and Species Groups

Species database—A total of 1,347 individual terrestrial species and 93 species groups of plants and animals were represented in a species-environment relations (SER) database (Marcot 1997; Marcot and others 1997). These are not all the individual species or species groups that occur in the basin assessment area but includes rare or potentially rare plants, selected invertebrates, and all vertebrates.

The SER database includes descriptions of (a) key environmental correlates of species, which consist of macrohabitats (vegetation cover types and structural stages) and other microhabitat and environmental factors that affect the presence, distribution, and realized fitness of species; (b) KEFs of species; (c) ecological status, including degree of endemism and geographic distribution of species; (d) legal listing status of species by various Federal and State agencies; and other information.

Species groups included lichens, bryophytes, vascular plants, bacteria, protozoa, rotifers, and nematodes. Species of lichens and bryophytes were grouped according to common use of substrates or soil conditions. Species of vascular plants were grouped based on various criteria, including genera difficult to identify, taxonomic uncertainty, and taxa for which knowledge and experts were available. Some vascular plant groups likely are either underrepresented or not represented in some geographic areas. Thus, although we summarize number of vascular plant groups, we do not include them in subsequent ecological analyses. Bacteria, protozoa, rotifers, and nematodes were each grouped according to their presence and ecological function in soils.

In the SER database, information on rare or potentially rare plants also included life form, categories of population trend (as denoted in state Natural Heritage databases), dispersal mode, pollinators, indicators of specific soil or environmental conditions, and occurrence by state, general geographic area, substrate, and local topographic condition (azimuth, relief, and slope). Information on invertebrates also included dispersal mode. Information on vertebrates also included percentage of overall distributional range of each species occurring within the basin assessment area, and the breeding, seasonal occurrence, and abundance status of birds.

The SER database was queried to produce ecological profiles of species by taxonomic group, habitat condition, ecological function, ecological status and geographic occurrence, legal status, and other attributes. Because few studies have been conducted on most of the basin species, the SER database is incomplete and consists largely of categorical information based on the judgments and experiences of experts (see Marcot and others [1997] and Marcot [1997] for caveats on use and interpretation of the SER database information).

Plants and allies—Occurrence and autecology of fungi, lichens, bryophytes, and vascular plants of the basin assessment area were summarized in Marcot and others (1997) and will be detailed in several other publications. In this report, number of taxa and species groups of plants and allies were tallied by life-form category, population trend class, geographic occurrence, substrate, local topographic condition, dispersal mode, type of pollinator, and type of indicator function. Life-form categories of plants followed the classification of Raunkaier (1934). Information in the SER database on plant dispersal modes was entered as comments taken from experts; the comments were then coded into categories, as discussed in "Results." Trends of vascular plant species, and of lichen, bryophyte, and vascular plant groups were denoted in four categories (unknown, decreasing, stable, and increasing) by the Plant Task Group of the Science Integration Team. In this document, only scientific names are used for plants, as common names have not been standardized.

Invertebrates—Ecology of invertebrates of the basin assessment area was noted in Marcot and others (1997), summarized in Niwa and Sandquist (in prep.), and will be detailed by functional group in several other publications. In this report, dispersal modes of example invertebrate species of the basin assessment area were categorized and cross-tabulated with KEFs of species. This helped determine the role of dispersal ecology in maintaining ecological functions of the invertebrate fauna. Examples of invertebrate species and micro-organism groups dispersing by phoresis (by using another organism as a dispersal host) were listed, illustrating how species interactions have evolved that potentially influence viability and distribution of some invertebrates and micro-organisms.

Vertebrates—Ecology of vertebrates of the basin assessment area was summarized in Marcot and others (1997) and will be detailed by selected species groups in other publications. In this report, patterns of taxonomic diversity were explored by tallying number of species, genera, and families through the basin assessment area and by vegetation cover types and structural stages.

Key ecological functions of species were further explored by cross-tabulating number of vertebrate species by ecological functions and by terrestrial vegetation communities. This resulted in "species-function profiles" that were used to determine which vegetation communities had the greatest variation in KEFs of species, and which ecological function categories varied the most over vegetation communities.

Species function profiles were developed for all vertebrates combined by tallying the number of species with selected specific KEFs, by terrestrial vegetation community. Greater numbers of species with the same KEF in a specific community were interpreted as greater redundancy of that function. Similarly, Huston (1994:3) referred to species with the same KEFs as "functional types of organisms," and redundancy of species with a particular KEF as "functionally analogous species." Franklin and others (1989:93) noted that "forest ecosystems which have redundancy in structure and function are more likely to be able

to absorb stresses, including species losses, without catastrophic damage. . . ." Silver and others (1996:17) similarly concluded that "functional diversity, and not just species richness, is important in maintaining the integrity of nutrient and energy fluxes," and that high species richness affords alternative and redundant pathways for the flow of resources in an ecosystem. Our species function profiles helped (1) identify communities with the greatest (and the least) redundancy in ecological functions of species, and (2) determine variation in redundancy of each KEF among communities.

Total functional diversity of all vertebrate species was calculated by multiplying the number of KEFs of vertebrate species in each terrestrial vegetation community by the average number of vertebrate species performing each function (after Huston 1994:4ff). Species function profiles and total species functional diversity were not calculated for rare or potentially rare plants and allies, nor for invertebrates, because (a) scientific knowledge and our databases of these taxa are incomplete, and (b) most of these species likely respond to microhabitats, microclimates, and substrates at far too fine a resolution than afforded by the available broad-scale data in this study.

Broad-scale ecological distribution of birds was assessed by cross-tabulating number of bird species by abundance, breeding status, migration status, and U.S. state, and relating to general geographic location. Five abundance categories and five breeding or migration status categories were denoted for birds (appendix A). Bird species abundance, breeding status, migration status, and occurrence by U.S. state were examined for patterns of local and regional endemics (see Marcot and others [1997] for definitions of endemism classes used with plants and animals).

We explored potential effects of regional climate change[2] on vertebrates. We first listed species associated with vegetation communities that may undergo major declines in distribution and area under climate-change scenarios. We then tallied the number of vegetation cover types used by each species and rank-ordered the species in increasing number of cover types used. We iden-

tified species at risk as those that use <20 percent (and also those species at greater risk that use <10 percent) of the total number of vegetation cover types (N = 44). These are species closely associated with the primary vegetation community of interest and are thus at greatest risk of decline or extirpation from climate-induced changes of that community.

Present and Past Terrestrial Characterization of the Basin Assessment Area

Present character—The Science Integration Team described broad-scale characteristics of the basin assessment area in terms of vegetation cover types and structural stages, geology, weather, land form, and other attributes, by 1-km^2 cells, 4th-code HUCs, and 6th-code HUCs (chapters in Quigley and Arbelbide 1997).

Historic character—We used results of reconstructions of early historic (early 1800s) vegetation conditions and changes to current conditions, as provided in Hann and others (1997).

Prehistoric character—In this report, we also summarize aspects of paleoclimates and paleoecology of the basin assessment area by comparing reports of prehistoric climates and biota with those of the present. We compared diversity of vertebrate Tertiary paleofaunas with that of modern faunas in eastern Oregon, at order, family, genus, and species levels of taxonomy and by geologic period, and drew conclusions on qualitative changes in environments, turnover of various taxa, and changes in overall terrestrial communities. Data are lacking on prehistoric rates of species extinction and speciation in the basin assessment area.

Assessment of Ecological Integrity of Terrestrial Species and Communities

Ecological integrity refers to the degree to which native taxa and their ecological functions persist under human land management (for example, Majer and Beeston 1996). Ecological integrity was assumed by the Science Integration Team to be a general purpose for managing ecosystems. Ecological integrity reflects the degree to which all ecological components and their interactions

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[2] Personal communication. Sue Ferguson, Climate model data, Forestry Sciences Laboratory, Seattle WA 98105-6497.

are present and functioning. We assumed that the six goals of managing for ecological integrity in land use planning, as discussed by Haynes and others (1996), provide important benchmarks against which to measure progress. Three of those goals dealt explicitly with terrestrial ecological conditions: maintaining species viability, maintaining long-term evolutionary potential of species, and managing for multiple ecological domains and evolutionary timeframes. We assumed that those three ecological goals could be interpreted in terms of species management objectives by using spatially referenced information on terrestrial species ranges and habitat and environmental conditions. In this way, conditions in 6th-code HUCs were mapped in a GIS (ArcInfo), for each component of terrestrial ecological integrity. Specifically, we followed these steps:

1. Reiterate the six goals for ecological integrity as identified by Haynes and others (1996) and identify those pertinent to terrestrial ecology (goals 1-3).

2. Under each ecological integrity goal, identify components pertinent to terrestrial ecology, particularly those that can be mapped and quantified. Denote these components under each of the three goals pertinent to terrestrial ecological conditions (as discussed in Marcot and others 1997).

3. For each integrity component, identify corresponding species by querying the SER database. Then identify the set of GIS map themes, including distributions of species, to represent the component.

4. For each integrity component and its set of GIS map themes, quantify conditions for each 4th code HUC in the basin assessment area. Use these data to build a database in which rows are individual 4th code HUCs, columns are the integrity components, and cells are filled in based on counts, percentages of each HUC covered, or other measures pertinent to each component.

5. Produce a map for each integrity component showing, by 4th code HUC, the outcome of combining all relevant GIS themes as defined in step 4.

6. Merge the database from step 4 with similar data on 4th code HUCs into an overall database expressing combined conditions for all terrestrial ecology components of ecological integrity.

Overall results were expressed in three maps depicting current average conditions for each of the three ecological integrity goals pertaining to terrestrial species and ecosystems. These maps are intended to provide a broad-scale overview of the basin assessment area that may be useful in planning policy. They are not scaled for site-level or midscale management use.

Chapter 4

Results

Further Explorations of Terrestrial Biodiversity

Marcot and others (1997) present a preliminary summary of biodiversity patterns of species among taxonomic groups within the basin assessment area. In this section, we expand on those findings.

First, how does biodiversity within the basin assessment area compare with global patterns? Estimated global biodiversity suggests that most species are insects (fig. 10, Wilson 1988). Next in estimated global abundance are algae (not tallied for the current work), bacteria, fungi, nematodes (roundworms), spiders and mites, and other taxa. The least abundant taxa globally are vertebrates (fig. 10). Estimates of diversity in the basin assessment area suggest that most species are bacteria, followed by fungi, macroinvertebrates (insects), plants and allies (lichens and bryophytes), and other species. The least abundant in the basin assessment area are soil nematodes[1] and vertebrates (fig. 11).[2] Overall patterns indicate that, both globally and in the basin assessment area, estimated species diversity (number of species) of invertebrates and micro-organisms rank highest and vertebrates lowest.

On comparing known with estimated species diversity, it is obvious that the largest gap in scientific knowledge (less than half of estimated numbers of species actually known) globally occurs with meso- and micro-organisms. The best known taxa are vertebrates. In the basin assessment area, the least known taxa probably include most of the micro-organisms, as well as insects, fungi, and mollusks. Only 14 percent of the estimated number of insect species in the basin assessment area have actually been reported from the basin assessment area. The percentages for fungi (33 percent) and mollusks (49 percent)[3] are a little greater. (Percentage values presented here are approximations.) Globally, the percentage of estimated number of species (from the upper estimate values) that actually are known are 0.13 percent of bacteria, 0.95 percent of insects, 1 percent of viruses, 5 percent of fungi, 8 percent of spiders and mites, and 35 percent of mollusks. Thus, on a percentage basis, these taxa are better known in the basin assessment area than they are globally, although much basic work on species inventory and taxonomic studies remains to be done.

The best known taxa (at least half of estimated number of species actually known) in the basin assessment area probably are vertebrates and lichens (all or nearly all likely occurring species have probably been discovered and catalogued in the basin assessment area), followed by vascular plants (99 percent or perhaps a bit less) and bryophytes (94 percent). Globally, the best known taxa are vertebrates (90 percent) and vascular plants (50 percent). Most of the biodiversity patterns of

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[1] That nematodes rank high in global biodiversity and low in the basin assessment area likely reflects how poorly known they are in the basin assessment area rather than their true abundance. All the values of known and estimated species biodiversity are subject to change as new studies are initiated.

[2] This comparison between global and basin assessment area biodiversity is not strictly at parity, because data on all taxonomic groups as divided for the basin assessment area analysis were not available at a global level.

[3] No figures for these percentages are available for micro-organisms in the basin assessment area. So little work has been done on these taxa that virtually all are unstudied and empirically undocumented in the basin assessment area.
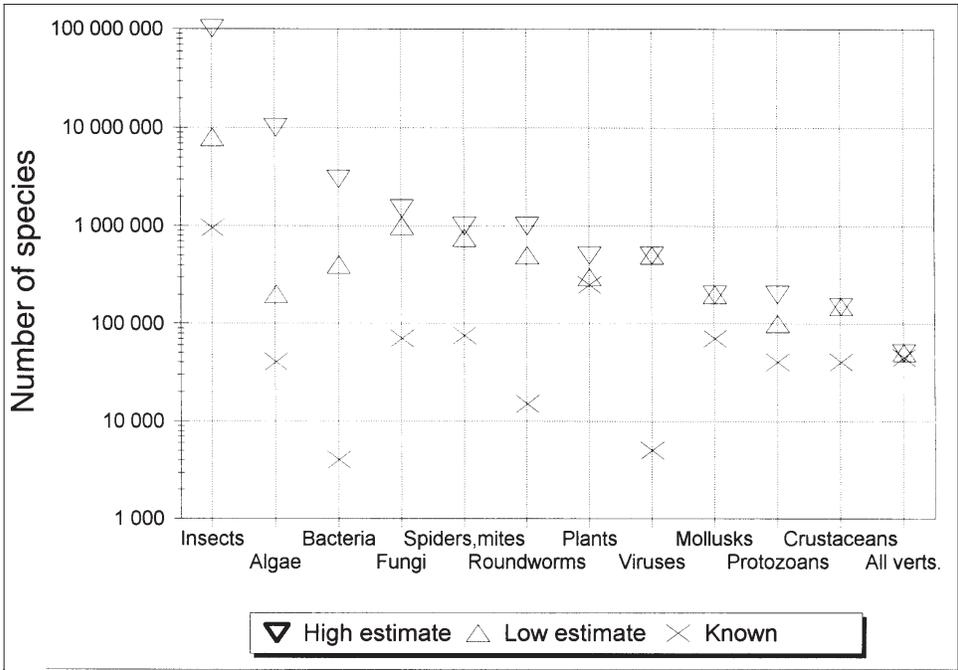
Figure 10—Diversity of terrestrial species globally, showing known, low estimates, and high estimates of number of species by taxonomic class, sorted in decreasing order of high estimates (source: Marcot and others 1997). (Note log scale.)
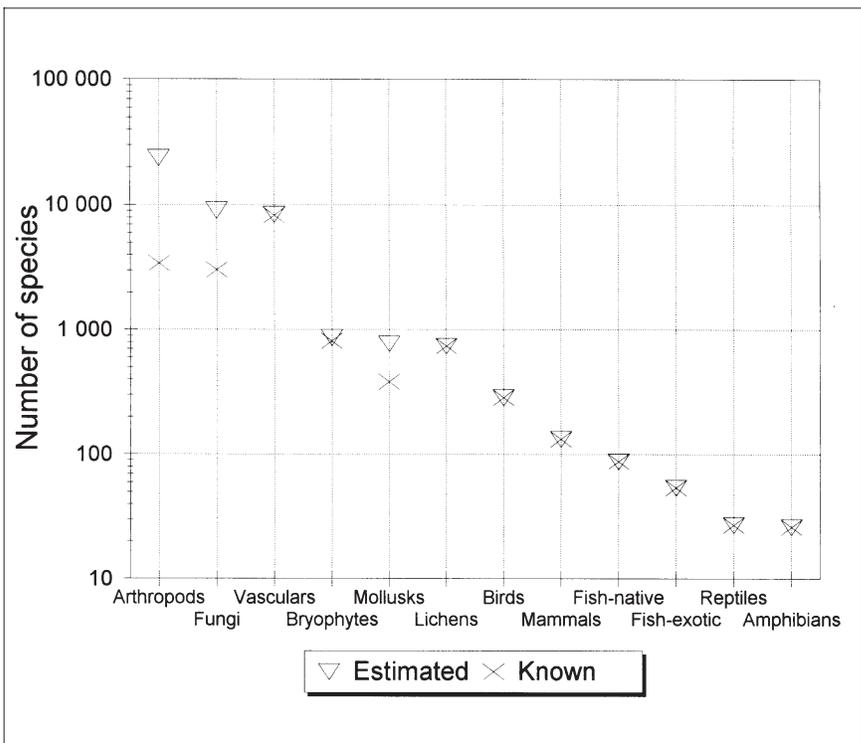

Figure 11—Diversity of terrestrial species and fish in the basin assessment area, showing known and estimated number of species by taxonomic class, sorted in decreasing order of estimated number. (Note log scale.)

species numbers by major taxonomic groups in the basin assessment area follow global patterns. Some groups are better known in the basin assessment area because the global estimates are weighted heavily toward largely unstudied tropical ecosystems.

Macroecology of Individual Species and Species Groups

Plants and Allies

Number of species—In the basin assessment area, some 18,946 species of plants and allies are estimated to exist (Marcot and others 1997). This figure extrapolates for species not yet discovered or catalogued and includes projections of about 9,000 species of macrofungi, 736 lichens, 860 bryophytes, and 8,350 vascular plants. At present, only 12,797 species of plants and allies (68 percent of all estimated species) are actually known from the basin assessment area, including about 3,000 macrofungi (33 percent of all estimated macrofungi species), 736 lichens (100 percent of all estimated lichens), 811 bryophytes (94 percent of all estimated bryophytes), and 8,250 vascular plants (99 percent of all estimated vascular plants). An additional large set of microfungi, including mycorrhizae, likely occur but are largely unstudied and are not treated here.

The SER database lists 596 individual taxa (mostly species with selected subspecies or varieties) and 82 species groups of plants and allies. These include 394 species of macrofungi; 2 species and 39 groups of lichens; no species and 11 groups of bryophytes; and 200 taxa and 32 groups of vascular plants (one part of the SER database also lists 920 vascular plant taxa, but information on environmental correlates and ecological functions are not available for all of these taxa.) The 596 taxa and 82 groups mostly represent rare or potentially rare but largely unstudied taxa and communities; the vascular plants included are mostly perennial forbs or nonwoody perennials. Thus, the analyses that follow pertain only to this select subset of rare or potentially rare plants of the basin assessment area and do not represent conditions of the full flora.

Species and groups by geographic area—Presence by general geographic area within the basin assessment area was denoted for lichen groups, vascular plant groups, and vascular plant species. Numbers of lichen groups and vascular plant groups were relatively evenly distributed throughout most of the geographic areas, with fewer in Wyoming and Nevada probably because of the small total area these states occupy within the basin assessment area. Exceptions also include the Columbia Plateau, which is entirely contained within the basin assessment area but which had only two lichen groups represented, and the Basin and Range area (northern Great Basin), which extends well beyond the basin assessment area and had only one vascular plant group. The few numbers of these species groups may be an artifact of the grouping process.

Numbers of the rare and potentially rare vascular plant species considered in this assessment were less evenly distributed among general geographic areas (fig. 12) than were lichen groups and vascular plant groups. Geographic areas with more species (>25 species) included Basin and Range, Columbia Plateau, Blue Mountains, northern Idaho, and the southern part of the east side of the Cascade Range. Areas with fewest species (<10 species) included the small portion of Wyoming within the basin assessment area, southern Idaho, and Okanogan Highlands, although the last two of these areas were not reduced in number of species groups.

Life forms—Life forms of most of the rare or potentially rare fungi were mushrooms (59 percent of all 394 macrofungi taxa included in the SER database) and truffles (31 percent), with the rest puffballs (7 percent), polypores (2 percent), and resupinate (1 percent) (fig. 13; see definitions in table 4).

Life forms of most of the rare or potentially rare vascular plants were hemicryptophytes (36 percent of all 280 vascular plant taxa included in the SER database) and cryptophytes (30 percent), with the rest therophytes (16 percent), chamaephytes (15 percent), and phanerophytes (4 percent) (see definitions in table 4). Plants of most of these life-form categories are widely distributed among vegetation cover types of the basin assessment area. The hemicryptophytes (102 species) are found in 27 vegetation cover types, most
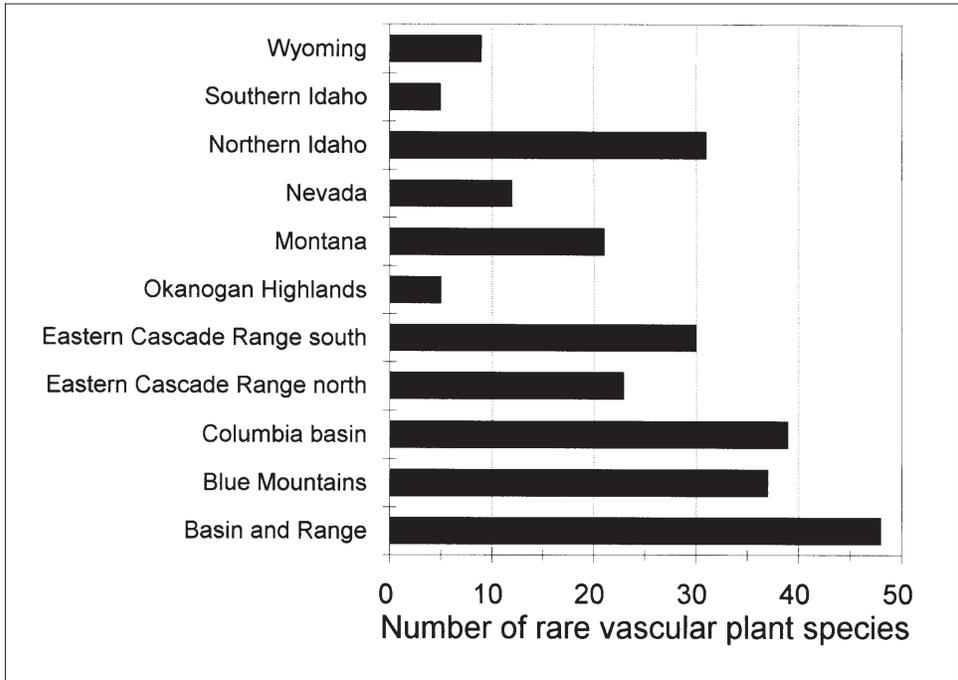
Figure 12—Number of rare or potentially rare vascular plant species by geographic area within the basin assessment area.
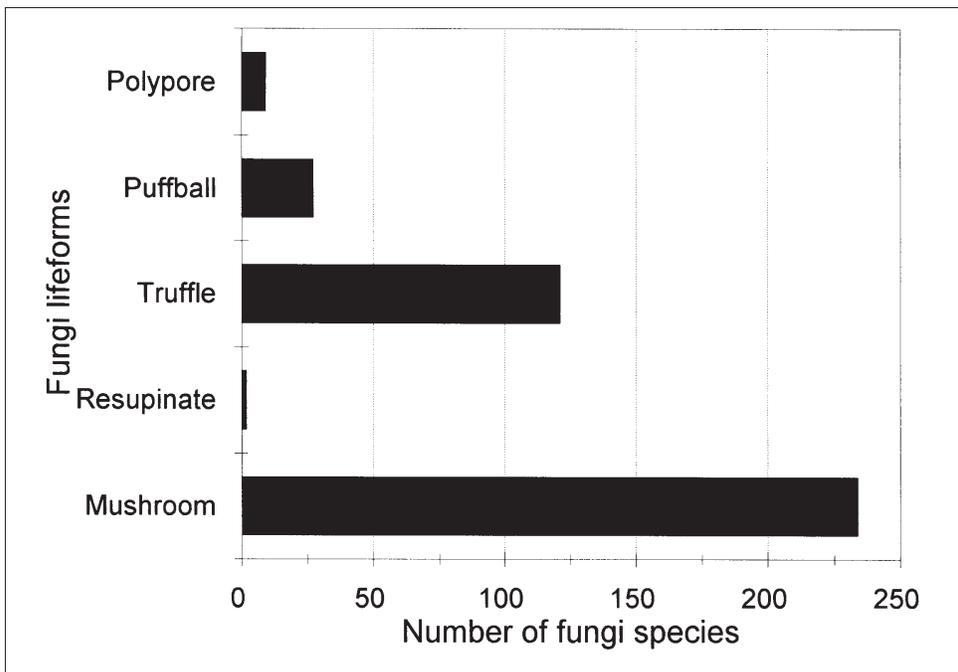

Figure 13—Diversity of macrofungi in the basin assessment area by life form (see table 4 for descriptions of life forms).

Table 4—Classes and definitions of fungi and vascular plant life forms[a]

Class	Definition
Fungi:	
Mushroom	Fungi with any macrofruiting body, typically those with cap and stipe morphology
Resupinate	Upside down or recurved growth form
Truffle	Fungi that are hypogeous (undergound), rare, odoriferous, and edible, of Ascomycetes
Puffball	Fungi of Gastromycetes of the order Lycoperdales (true puffballs and stalked puffballs); does not include Hymenogastrales (false puffballs)
Polypore	Fungi in the family Polyporaceae
Vascular plants:	
Phanerophyte	Species with perennating buds or shoot apices on aerial shoots. Group includes most woody shrubs or trees
Chamaephyte	Species that hold their perennating buds and shoot apices close to the ground. Group includes semiwoody and herbaceous species that persist aboveground throughout the year (though not necessarily in a physiologically active state). Group includes bunch grasses and cushion plants
Hemicryptotphyte	Species with perennating buds at ground level, generally protected by snow or organic debris, with all plant parts aboveground dying back at the end of the active growing season. Stolons may or may not be present. Group includes rosette plants (for example, *Taraxacum*), partial rosette plants (for example, *Achillea millefolium*), and stoloniferous species (for example, *Rubus*)
Cryptophyte	Species bear their perennating buds below ground level or submerged in water. Group includes rhizomatous and bulb-forming species (for example, *Allium*), and aquatic species such as *Alisma* and *Nuphar*
Therophyte	Annual species (for example, *Bromus tectorum*, *Stephanomeria malheurensis*). Embryonic buds are protected by a seed coat

[a] Fungi definitions from W. Owen. Vascular plant definitions from L. Croft based on Raunkier (1934); also see Daubenmire (1974).

principally in big sagebrush (26 species), low sage (14 species), mountain big sagebrush (13 species), fescue-bunchgrass (12 species), and alpine tundra (11 species), with the remaining 26 species distributed among 22 other vegetation cover types. The cryptophytes (84 species) are found in 22 vegetation cover types, most principally in fescue-bunchgrass (20 species), *Agropyron* bunchgrass (14 species), interior ponderosa pine forest (13 species), and juniper/sagebrush (10 species), with the remaining 27 species distributed among 18 vegetation cover types. The therophytes (45 species) are found in 21 vegetation cover types, most principally in big sagebrush (10 species), juniper sagebrush (9 species), interior ponderosa pine (9 species), and interior Douglas-fir (8 species), with the remaining 9 species distributed among 17 other vegetation cover types. The chamaephytes (42 species) are found in 21 vegetation cover types, most principally in low sage (13 species), big sagebrush (8 species), and mountain big sagebrush (5 species), with the remaining 16 species distributed among 18 other vegetation cover types. Finally, the phanerophytes (10 species) are found in seven vegetation cover types, most principally in *Agropyron* bunchgrass (two species) and low sage (two species), with the remaining six species distributed among three other vegetation cover types. These are very general patterns; information on finer classes of habitat types would reveal more useful botanical patterns.

Number of rare or potentially rare vascular plant species among life-form categories do not show a clear trend at the broad scale in relation to general topographic position, soil texture, soil depth, soil moisture regime, or soil temperature categories, although correlations would be expected at finer scales of resolution. This is not surprising, given the very microsite- and substrate-specific nature of most of these rare or potentially rare plants. Based on the initial assignments of plants to life-form categories, hemicryptophytes might occur more frequently in calcareous substrates than do other life forms; they also might occur most commonly in alkaline soil conditions. This may represent an ecological pattern, or merely reflect the dominance of this life form in the rare plant flora. These patterns need verification and further ecological study.

In general, alkaline or calcareous soils are typically rich in edaphic endemics worldwide. Most plant species are unable to overcome the physiological challenges imposed by such soils, including Ca^{++}/Mg^{++} imbalances and the general low availability of nitrogen, phosphorus, and potassium nutrients in high pH situations because of specific solubilities. Alkaline or calcareous sites tend to be azonal; that is, represented by an intrusion into a matrix of some other parent material (for example, granite or sandstone). Those plants that thrive in such azonal settings with few other species capable of surviving the local conditions often have an opportunity to escape competition. Azonal soils almost always have unique, if not rare, flora. Examples include serpentine or ultramafic conditions in northwestern California and southwestern Oregon, volcanic ash in eastern Oregon and western Idaho, and hyperacidic mine tailings, hot springs, and sandy substrates elsewhere. Specialization of rare or endemic plants to azonal conditions can be considered an extreme form of habitat segregation.

Trends of vascular plant species—Of 299 rare or potentially rare vascular plant species, 143 species (48 percent) had unknown or unreported trends, 84 species (28 percent) were coded as decreasing, and 71 species (24 percent) as stable. One species (<1 percent) might be increasing at least in some areas. Among the decreasers were various species of *Allium, Aster, Astragalus, Botrychium, Calochortus, Cypripedium, Eriogonum, Haplopappus, Howellia, Lepidium, Mentzelia, Mimulus, Penstemon, Ranunculus, Silene, Thelypodium, Trifolium,* and other genera. Among the stable species were various other species of *Allium, Astragalus, Botrychium, Castilleja, Claytonia, Erigeron, Eriogonum, Leptodactylon, Mentzelia, Mimulus, Penstemon, Trifolium,* and other genera. The sole potential increaser was an *Astragalus* species. Species with unknown or unreported trends spanned an even greater number of genera.

Trends of lichen, bryophyte, and vascular plant groups—Trends were denoted for lichen groups, bryophyte groups, and vascular plant groups (fig. 14). Trends of most of the lichen groups were decreasing (41 percent of all lichen groups) or stable 36 percent), with fewer groups having unknown or unreported trends (18 percent) or increasing trends (5 percent). Trends of
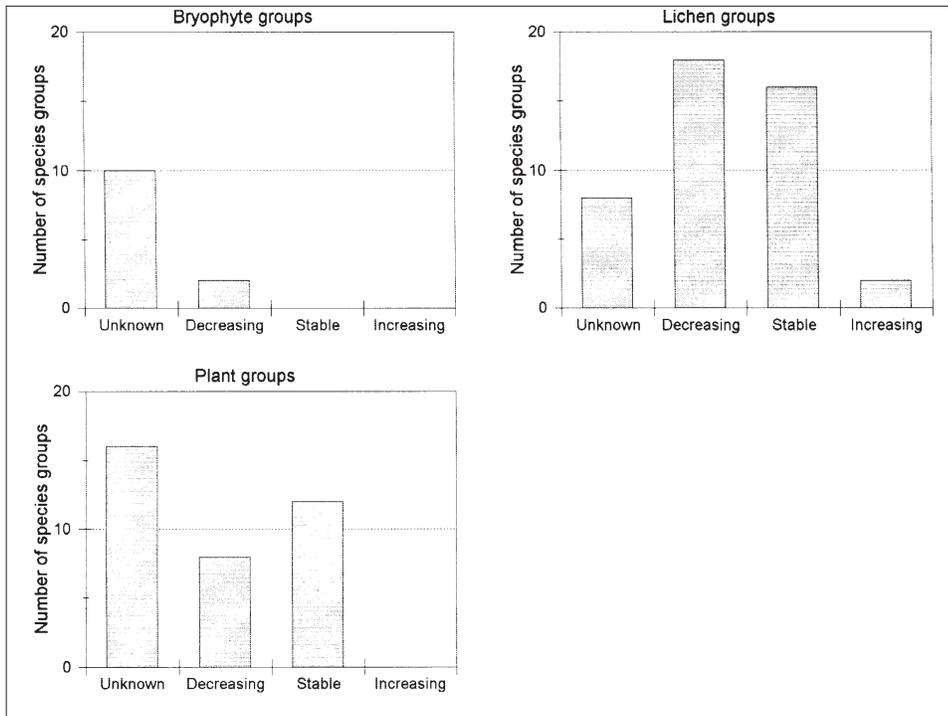
Figure 14—Number of lichen, bryophyte, and vascular plant species groups in the basin assessment area, by trend category.

bryophyte groups were largely unknown or unreported (83 percent of all bryophyte groups), with fewer decreasing (17 percent); none was stable or increasing. Trends of vascular plant groups were mostly unknown or unreported (44 percent of all vascular plant groups), with fewer groups stable (33 percent) or decreasing (22 percent); none was increasing.

The only two lichen groups noted as having increasing trends were excess nitrogen-indicator lichens and urban pollution-tolerant lichens.

The 28 stable groups included 16 lichen groups in various aspen, calcareous, fencepost, leaf, rock, seepage, ledge, and tundra conditions and substrates, and 12 vascular plant groups consisting of 2 *Allium* groups, 5 *Mimulus* groups, and 5 *Penstemon* groups.

The 28 decreaser groups included 18 lichen, 2 bryophyte, and 8 vascular plant groups in various arid, riparian, and forest conditions. The two decreaser bryophyte groups included the decayed wood bryophyte group and the epiphytic bryophyte group.

The 24 lichen groups with unknown or unreported trends included 3 lichen groups of bog, nitrogen fixation, and pioneer soil stabilizer conditions; 9 bryophyte groups of aquatic, humid duff, peatland, rock, and soil conditions; and 12 vascular plant groups, all *Carex* groups mostly of meadows association, with a few of peatland and forest conditions.

Lichen, bryophyte, and vascular plant species groups by substrate—Lichen, bryophyte, and plant groups included in the SER database were denoted with orientations to specific nonvegetation substrates and vegetation substrates.

Patterns of species groups among nonvegetation substrates were as follows: lichen groups were more numerous on basalt rock, other rock, and welded tuff; bryophyte groups were fairly evenly distributed among all substrates but were absent on pumice and welded tuff (fig. 15). Among all taxa, wet and dry soil substrates, and basalt and other rock substrates were used by the most species groups, and pumice and alkali soils were used by the fewest species groups (fig. 15). The composition of species groups, however, differed among these sets. For example, the sole lichen
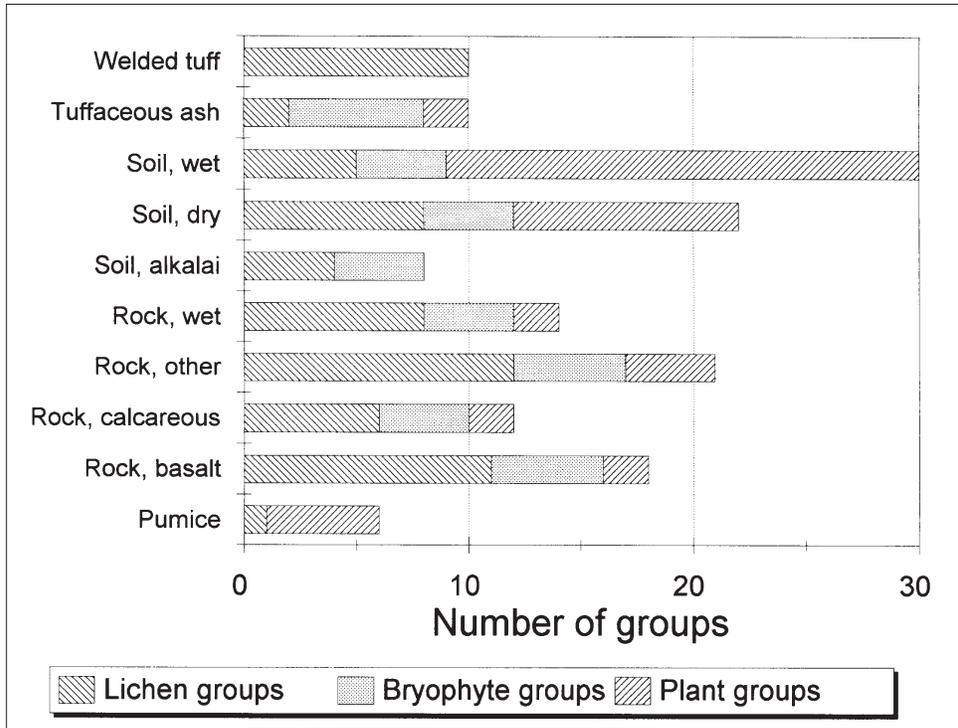
Figure 15—Number of lichen, bryophyte, and vascular plant species groups by soil and rock (nonvegetation) substrate condition in the basin assessment area.

group found associated with pumice substrates was the calcareous indicator lichens group. This group also is found on five other nonvegetation substrates. The two lichen groups—the pioneer soil stabilizer lichen group and the soil lichen group—associated with tuffaceous ash each also are found in three other nonvegetation substrates (dry, wet, and alkali soils).

Patterns of species groups among vegetation substrates were as follows: lichen groups were most numerous as epiphytic conditions and were absent in peatland, fen, and bog substrates (although individual lichen species may occur in such conditions); bryophyte groups were most numerous in aquatic submerged substrates but occurred in all but musicolous substrates; and vascular plant groups were most numerous in peatland, fen, and bog substrates and also occurred in humus and duff substrates but were not identified for the other vegetation substrates (although individual species occur on such substrates) (fig. 16).

Patterns of plant endemism—There are many examples of endemic plants in the basin assessment area. Some examples are Idaho goldenweed

(*Haplopappus aberrans*) in the Boise River drainage, *Chaenactis evermannii* Greene in central Idaho, and *C. nevii* Gray in the John Day area.

Not all endemic plants are rare, and not all rare plants are endemics. A large proportion of the rare or potentially rare plants considered in this assessment, however, are locally endemic or regionally endemic (156 taxa or 78 percent of 200 vascular plant species in the SER database with information on endemism status). We defined local endemic as a plant with populations restricted to a very small area such as one portion of a mountain range or one canyon. Local endemics also may be specialized on highly restricted habitats. The entire range may lie within the basin assessment area. A regional endemic is a plant with populations that inhabit a larger geographic area than that of local endemics such as southeast Oregon or the Palouse. The range of regional endemics may extend beyond the basin assessment area boundaries. Regionally endemic plants also may be closely associated with specific habitats. In general, about a third of all vascular plants (including common and rare species) are endemic at least regionally.

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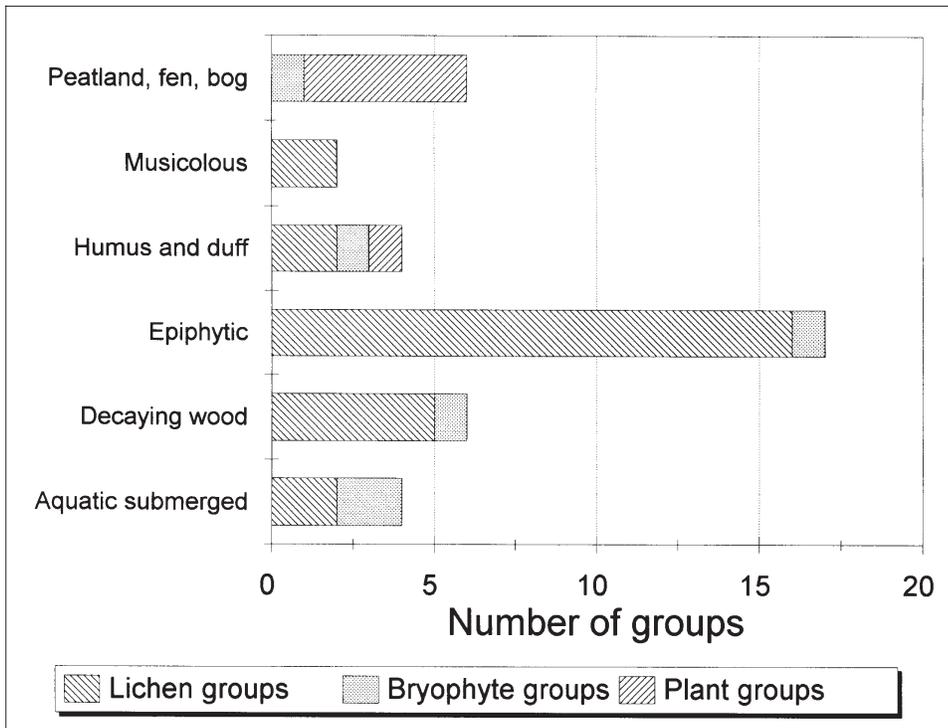
Figure 16—Number of lichen, bryophyte, and vascular plant species groups by vegetation substrate condition in the basin assessment area.

Gentry (1986) tallied endemic plants (mostly based on candidate taxa for Federal listing, similar to our consideration of plants of conservation concern) by U.S. state. We compare our tallies with his in table 5. His definition of endemic taxa included plant species with distributions of 50 000 km^2 or less, which corresponds to our categories of local and regional endemics. His tallies included entire states, whereas ours included only portions of states within the basin assessment area. We counted more endemic plants in Idaho and Montana than he did, however; whereas his figures for Oregon, Washington, Nevada, and Wyoming were greater than ours. (We did not characterize plant endemism in the Utah portion of the basin assessment area.) Only a small portion of Nevada and Wyoming are within the basin assessment area, so these differences are not surprising. But we were surprised to see our greater tallies for Idaho and Montana, considering particularly that only the western portion of Montana (west of the Continental Divide) was included in the basin assessment area, and only a portion of the entire flora of the basin assessment area is included in the SER database. Our greater

tallies of endemic plants in Idaho and Montana possibly reflect more current data from state Natural Heritage program databases.

Gentry (1986) suggested two kinds of endemics. The first kind is **paleoendemics**, which are species that were formerly more widespread but now have restricted distributions because of climatic changes and natural or human-caused reduction of favorable habitats. Some paleoendemics may be archaic taxa with primitive traits; some may be close to natural extinction. Pielou (1991:240) notes that the present alpine flora of the western mountains contains a mix of paleoendemic plant species, some presumably derived from Pleistocene refugia south of the Cordilleran ice sheet and others from northern Beringian tundra. She also noted that the nearest unglaciated drainage basin to the Cordilleran ice of the Pleistocene was that of the Columbia River, which must have been the refuge for many paleoendemic species.

The second kind of endemic is **neoendemics**, which are species that have recently evolved and have restricted ranges because they have not yet had time to spread over a larger geographic area. Examples of neoendemics might include species

Table 5—Tallies of locally and regionally endemic plant taxa in U.S. states of the basin assessment area, compared with estimates of endemic plant species from Gentry (1986:155)[a]

| State | This study | | | Endemics as listed by Gentry (1986) |
	Local endemics	Regional endemics	Total	
Oregon	47	30	77	109
Washington	24	13	37	49
Idaho	29	22	51	37
Montana	6	7	13	6
Nevada	2	1	3	19
Wyoming	1	3	4	90
Entire basin assessment area	93	63	156	—

— = no data

[a] We defined local endemic as plants with populations restricted to a very small area such as 1 portion of a mountain range or 1 canyon, and regional endemic as plants with populations that inhabit a larger geographic area such as southeast Oregon or the Palouse. Gentry defined endemic as plant species with distributions of 50 000 km^2 sor less, which corresponds to our categories of both local and regional endemics.

that have recently arisen on serpentine and ultramafic substrates. Most species of *Astragalus* in the basin assessment area likely are neoendemics. *Allium aaseae* (Ownbey) is a "classic" neoendemic.

Kruckeberg and Rabinowitz (1985) suggested that paleoendemics tend to have more than one disjunct population, whereas endemics confined to a single population can be either paleoendemics or neoendemics. This contention is untested for the regional or local endemic plants of the basin assessment area. Of course, one cannot assert the converse; plants with more than one disjunct population cannot be assumed to be a paleoendemic, any more than plants with a single population are endemics of either type.

In general, paleontology explains much about current plant species distributions, especially with respect to historic climates. Some plants of northern Idaho occur because of the Clearwater Maritime refugium found there. Southern Idaho and the portion of Wyoming in the basin assessment area are geologically young, and the few endemics found there are classic neoendemics

of species-rich genera (for example, *Astragalus*). Also, climate fluctuations over the last several million years in southern Idaho have been broad, thereby making it difficult for either mesophytes or xerophytes to persist over the entire period (Tausch and others 1993).

Overall, genetic data are needed to determine which other vascular plant taxa within the basin assessment area are paleoendemic or neoendemic. Chemical, physical, and biological properties of soils often constrain endemic taxa (Kruckeberg and Rabinowitz 1985). In some cases, rarity or range-restriction of a coevolved symbiont may account for endemism of plant taxa, particularly with a rare obligate pollinator but, again, this needs empirical study in the basin assessment area.

We explored the question of environmental determinants of endemic plants by comparing 13 biophysical factors between the 156 plant taxa from the SER database that were denoted as local or regional endemics to the remaining 44 plant taxa in the database denoted as neither local nor regional endemics. This analysis is pertinent only

to rare or potentially rare plant taxa and does not describe more common or widespread plant species. The biophysical factors included in this analysis were maximum elevation, minimum elevation, aspect, slope angle, slope position, geographic area, geology, landform, soil pH, soil texture, soil depth, soil moisture, and soil temperature. These factors were coded for each species in the SER database as categorical values. We used a log-likelihood ratio contingency test to analyze the null hypotheses that local and regional endemics do not differ from nonendemics, in number of species distributed among categories of each of these biophysical factors.

Results are presented in table 6. Only two biophysical factors—slope angle and slope position—were significantly different ($P < 0.05$) between endemic and nonendemic rare plants. Six other factors were marginal in significance ($0.05 < P < 0.10$): maximum elevation, aspect, geology, landform, soil pH, and soil moisture. Given the broad scale of the basin assessment area and coarse resolution of the categorical data denoted in the SER database, the marginally significant factors might be seen as working hypotheses of biophysical conditions that influence numbers of rare endemic plants. Finer grain and more quantitative data, as well as species-specific analyses, are needed to further unravel the factors inducing plant endemism in the basin assessment area. Also needed are further studies to explain the exclusion of endemics from more common habitats (Kruckeberg and Rabinowitz 1985).

Plant dispersal modes—Dispersal (dissemination) modes of all rare or potentially rare plants of the basin assessment area are not thoroughly studied, but those known were denoted in the SER database. Seven general dispersal mode categories were identified: gravity, wind (anemochory), water, insects, vertebrates (zoochory), growth or reproduction, and unknown. The vertebrates dispersal category was further divided into dispersal by birds, small mammals, large mammals, and not specified. The growth or reproduction dispersal category was divided into dispersal by dehiscence, bulbett scattering, spore dispersal, stolon, rhizome, vegetation growth, seed dispersal, and turion. Dispersal mode was denoted for lichen, bryophyte, and vascular plant groups, and for the rare or potentially rare species of fungi and vascular plants.

Any one group or species could have been coded as having one or more dispersal modes.

Gravity plays the major role in dispersal of nearly all the lichen groups, with one other group (aquatic rock lichens) dispersing by water and by vertebrates (birds) (fig. 17). Dispersal modes of bryophyte groups were evenly split between water and wind.

About two-thirds (69 percent) of the 394 rare or potentially rare fungi species included in the assessment disperse by wind, and the remainder disperse by vertebrates (that is, mycophagy) (fig. 18). Mycophagy, or the ingesting and distributing of belowground fungal bodies (truffles) including spores, is an important ecological role of some large and small vertebrates in several forest types throughout the inland West. Vertebrates engaged in mycophagy and dispersal of fungi include Rocky Mountain elk (*Cervus elaphus nelsonii*), western red-backed vole (*Clethrionomys californicus*), southern red-backed vole (*C. gapperi*), northern flying squirrel (*Glaucomys sabrinus*), least chipmunk (*Tamias minimus*), Douglas squirrel (*Tamiasciurus douglasi*), American pika (*Ochotona princeps*), and Columbian mouse (*Peromyscus keenii*).

Dispersal modes of vascular plant groups included all seven major dispersal categories. Most vascular plant groups, however, disperse mainly by gravity, wind, water, and vertebrates (fig. 17).

The rare or potentially rare vascular plant species disperse (in order of decreasing number of species per dispersal category) by gravity (27 percent of species), wind (26 percent), growth or reproduction (21 percent), vertebrates (13 percent), water (7 percent), and insects (2 percent). How the remainder disperse (4 percent) is unknown (fig. 18). The 55 vascular plant species that disperse by vertebrates more or less evenly disperse by birds and small mammals, with fewer species dispersing by large mammals, and a third not specified (fig. 19a). Over half of the 89 vascular plant species that disperse by growth or reproduction do so by seed set; the remainder disperse by many other vegetative and reproductive means (fig. 19b). It must be remembered, though, that these patterns pertain only to the set of rare or potentially rare plants considered in this assessment, and that patterns of the full flora—

Table 6—Results of log-likelihood ratio contingency tests (*G* statistic) of bio-physical factors and endemic plants[a]

Biophysical factor	Value of *G*	df	P
Maximum elevation:	6.678	3	0.05 < P < 0.10 +
<1219 meters			
1219 to 1828 meters			
1829 to 2438 meters			
2439+ meters +			
Minimum elevation:	1.443	1	0.10 < P < 0.25
<1219 meters			
1219+ meters			
(Categories combined because of			
small sample sizes)			
Aspect:	7.781	4	0.05 < P < 0.10 +
North			
South			
East			
West			
Flat			
Slope angle:	7.929	3	0.025 < P < 0.05 *
Flat (0 to 10 percent)			
Gentle (11 to 30 percent)			
Steep (31 to 50 percent)			
Very steep (>50 percent)			
Slope position:	7.155	2	0.025 < P < 0.05 *
Lower slope			
Middle slope			
Upper slope			
Geographic area:	11.743	7	0.10 < P < 0.25
Basin and range			
Blue Mountains			
Columbia basin			
East Cascade Range north			
East Cascade Range south			
Montana			
Northern Idaho			
Southern Idaho			
(Other states omitted because of			
small sample sizes)			
Geology:	16.178	10	0.05 < P < 0.10 +
Basalt			
Calcareous			
Clay			
Glacial			
Granite			
Playa			

Table 6—Results of log-likelihood ratio contingency tests (*G* statistic) of bio-physical factors and endemic plants[a] (continued)

Biophysical factor	Value of *G*	df	P
Rhyolite			
Sand			
Sedimentary or metamorphic			
Slides and talus			
Tuff			
(Serpentine was omitted because of small sample sizes) +			
Landform:	7.111	3	0.05 < P < 0.10 +
Cliff			
Ridgetop			
Scablands			
Valley bottom			
Soil pH:	3.075	1	0.05 < P < 0.10 +
Acidic to neutral (combined because of small sample sizes)			
Alkaline			
Soil texture:	1.363	2	0.50 < P < 0.75
Coarse (sand)			
Medium			
Fine			
Soil depth:	3.896	3	0.25 < P < 0.50
Very shallow (<25 centimeters)			
Shallow (25 to 50 centimeters)			
Moderately deep (51 to 102 centimeters)			
Deep to very deep (>102 centimeters)			
Soil moisture:[b]	6.434	3	0.05 < P < 0.10 +
Andic			
Udic			
Ustic			
Xeric			
Soil temperature:[b]	0.144	2	0.90 < P < 0.95
Cryic (0 to 8 ℃)			
Frigid (diff. mean summer/ winter ≥ 5 °C)			
Mesic (8 to 15 ℃)			

[a] The null hypothesis for each test was that biophysical characteristics of locally and regionally endemic rare or potentially rare vascular plant species do not differ from those of nonendemic rare or potentially rare species.

[b] See Harvey and others (1994:3) for definitions of terms.
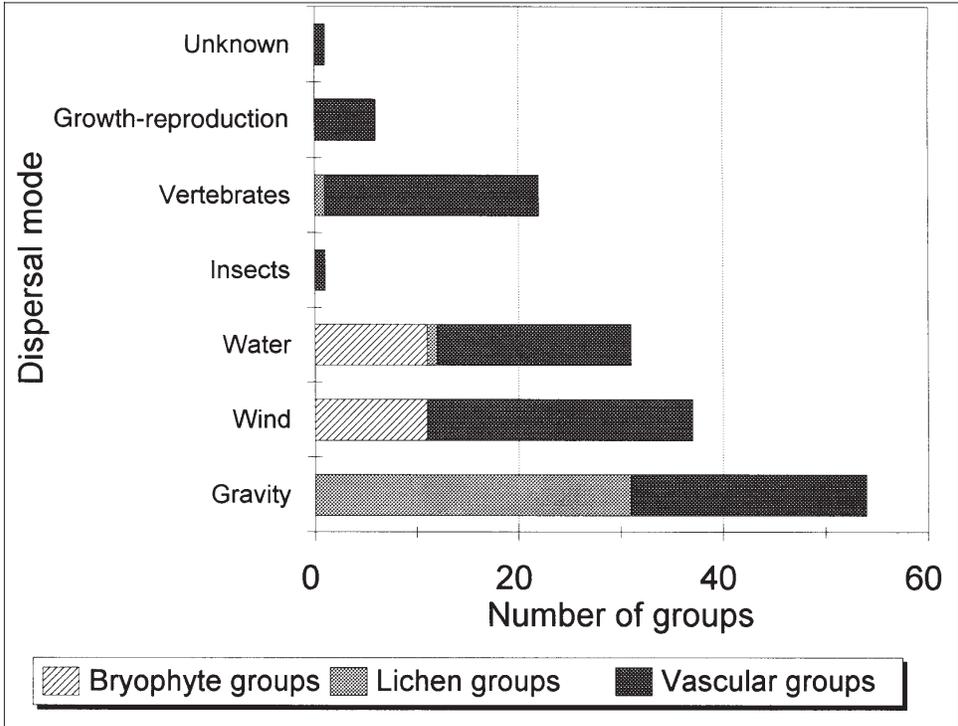
Figure 17—Number of lichen, bryophyte, and vascular plant species groups by dispersal mode.
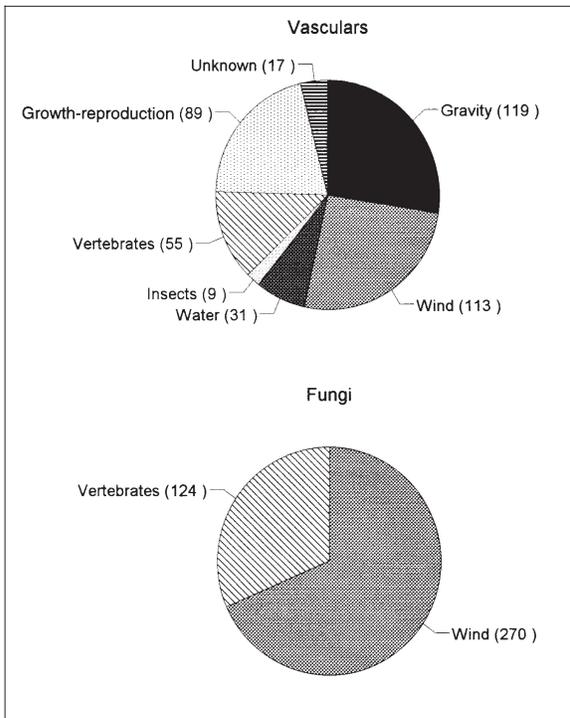
Figure 18—Number of rare or potentially rare fungi and vascular plant species by dispersal mode.
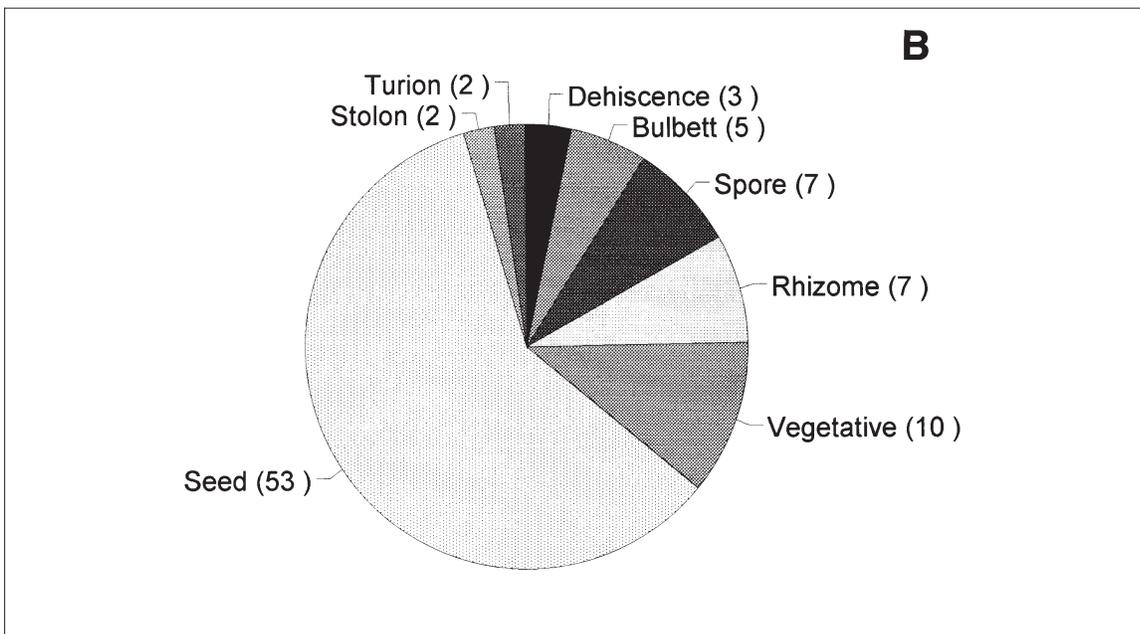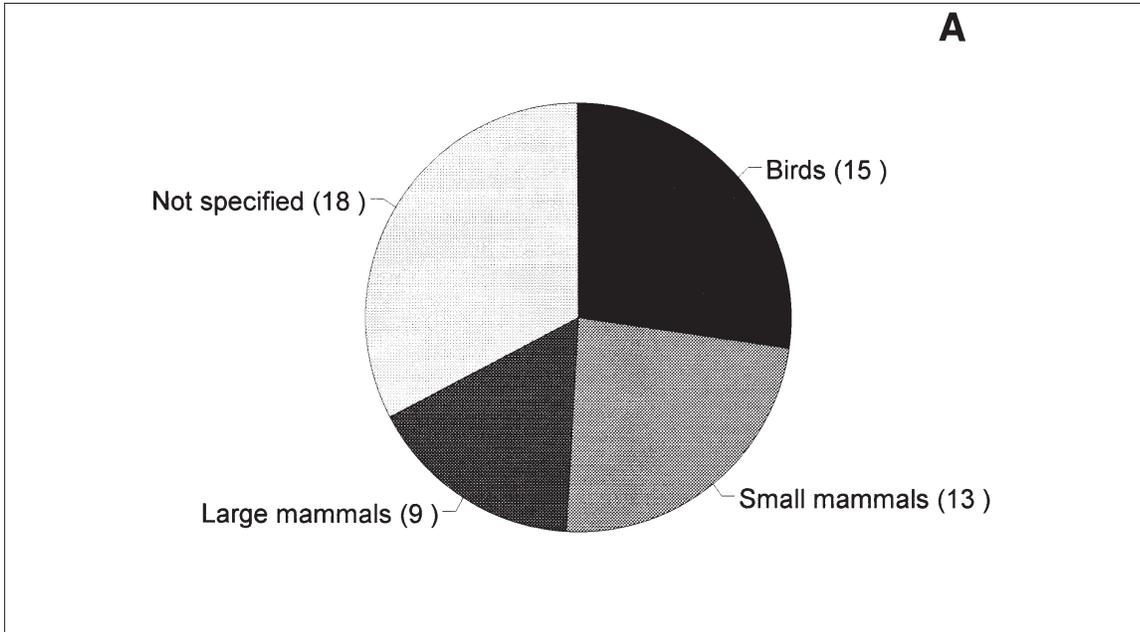
Figure 19—Number of rare or potentially rare vascular plant species by dispersal mode, showing (A) dispersal by means of vertebrates and (B) dispersal by means of growth or reproduction.

including many more trees, shrubs, and other forms—are likely to be very different.

Plant pollinators—Along with assuring suitable habitat conditions and protection of specific locations, successful pollination of the rare or potentially rare vascular plants of the basin assessment area may be one of the most important ecological factors that can help ensure their long-term viability. Pollination ecology of these species, however, is essentially unstudied and unknown. What follows are general patterns from initial presumptions as to pollination ecology. These patterns need to be tested with field studies.

As Buchmann and Nabhan (1996) note, plant-pollinator relations exemplify connections between endangered species and threatened habitats. Human-induced changes in pollinator populations—caused by overuse of chemical pesticides, unbridled development, and conversion of natural areas into monocultural cropland—can have a ripple effect on disparate species, ultimately leading to a "cascade of linked extinctions" (Buchmann and Nabhan 1996).

Pollinators also can be influenced by habitat fragmentation, sometimes differentially benefitting exotic insect pollination vectors to the detriment of native vectors. Aizen and Feinsinger (1994) studied native and honey bee (*Apis mellifera*; an exotic) pollinators of native flowering plants in subtropical dry forest of northwestern Argentina. They found that habitat fragmentation adversely affected native flower visitors but facilitated the use of floral resources by honey bees.

Loss of pollinators also can result in different selection pressures for reproductive strategies of surviving plants. In a modeling study of an isolated population of *Primula sieboldii*, Washitani (1996) reports that loss of pollinators may result in strong fertility selection for a self-fertile, homostyle morph. He concluded that active management of plants with absent or moribund pollinators could include hand pollinations and reintroduction and reestablishment of suitable pollinator populations. This would help maintain a more natural gene pool in future plant generations.

In the basin assessment area, by far most of the rare or potentially rare vascular plants are pollinated by invertebrates (66 percent of plant spe-

cies). Additional modes of pollination include autogamous pollination (10 percent), wind (5 percent), hummingbirds (2 percent), and generalist (1 percent), and others are unknown (16 percent) (fig. 20). Most plants are serviced by multiple pollinator species. For example, *Eriogonum prociduum* (prostrate buckwheat) likely is pollinated by beetles (Cleridae: Coleoptera) but also can be pollinated by flies (Tachinidae, Sarcophagidae, Bombyliidae: Diptera), wasps (six families: Hymenoptera), and moths (Sesiidae: Lepidoptera).[4]

Of the plants pollinated by invertebrates, about half are pollinated by bees, wasps, and allies (Hymenoptera), with others pollinated by flies (Diptera), butterflies and moths (Lepidoptera), beetles (Coleoptera), spiders (Araneida), and other insects (not specified) (fig. 21). Insects as a whole play a vital function in reproduction and viability of populations of angiosperms.

Long-term viability of many plant populations likely is affected by viability of plant pollinator and plant disperser mutualists. Many of these relations are typically highly specific (Menges 1991). Terbourgh (1986) discussed keystone mutualists, which are species that, if extinct, likely would result in secondary extinctions of many associated obligate species. Keystone mutualists might exist among insect-plant pollinator relations in the basin assessment area (and possibly also among plant-disperser relations as well). Thus, understanding basic pollination and dispersal ecology of plants is key to projecting and planning for long-term population viability.

Indicators—Plants and allies can serve as bioindicators of environmental conditions and ecosystem health. The concept is far from new, beginning perhaps with Clemment's (1920) usage of plant indicators to denote vegetation communities.[5] Others have extended the concept in various directions. For example, Nygaard (1949) indexed the trophic health and degree of eutrophication of water bodies by calculating the ratio in number of algae species of different taxonomic groups.

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[4] Source: OSDA-BLM Challenge Cost Share Project 89-6.

[5] Actually, well into prehistory, many indigenous peoples likely used plants to locate underground water, game animals, and good places to build camps. Modern science does not have the corner on observing nature.
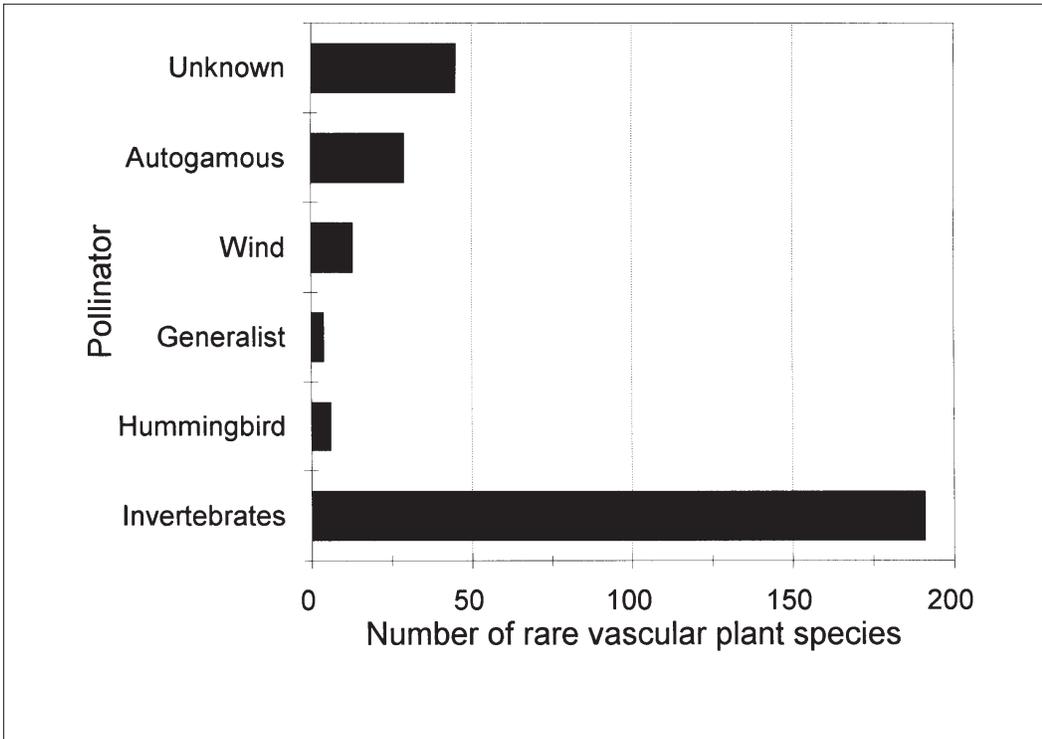
Figure 20—Number of rare or potentially rare vascular plant species by type of pollinator.
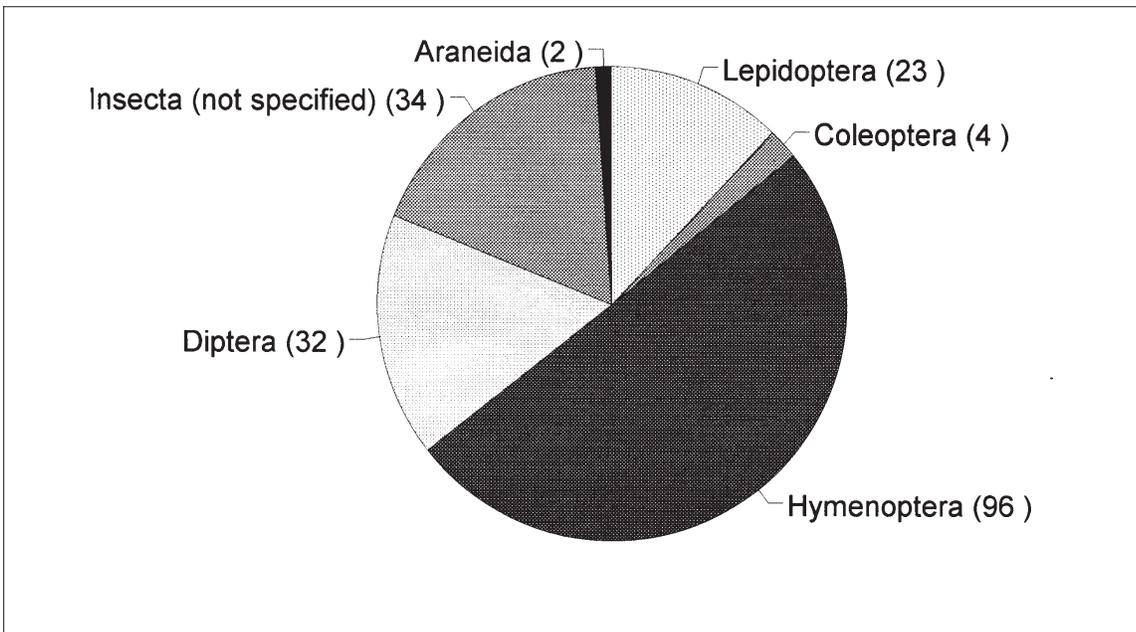

Figure 21—Number (in parentheses) of rare or potentially rare vascular plant species by type of invertebrate pollinator.

Westveld (1954) used plants to index site quality. And, Anderson (1986) (and many others) identified plant indicators of range condition.

The Plant Task Group of the Science Integration Team identified a number of lichen, bryophyte, and vascular plant groups and vascular plant species that can serve to index specific environmental conditions of the basin assessment area. Such environmental conditions include air quality, carbonate levels, water flow levels (low, high), high nitrogen conditions, metal-rich rock conditions, old-growth forest conditions, soil temperature (low, high), and soil texture (coarse, fine). Specific indicators, and the environmental condition for which they may be useful as an indicator, are listed in appendix B.

Overall, many lichens can be used to index air quality (fig. 22; see appendix B), a function already finding utility in management of many forests and other geographic areas (for example, Geiser and others 1994, Stolte and others 1993). Lichen groups along with bryophyte groups also can be used to index most of the other categories of environmental conditions listed above (fig. 22; see appendix B). In addition, vascular plant groups and rare or potentially rare vascular plant species can be used as bioindicators of alkaline (carbonate) soil conditions, overgrazing, metal-rich rock conditions, old growth, low soil temperature, coarse soil textures, and other conditions (fig. 22; appendices B and C).

Nonvascular plant indicators of old-growth forest conditions may be of particular interest to managers. Tibell (1992) identifies crustose lichens as indicators of temporal continuity of old boreal conifer forests. The term temporal continuity refers to the degree to which specific kinds of habitats—in this case, old boreal conifer forests—continuously occupy a local geographic area over time. Some studies outside the basin assessment area have indicated that interrupting the temporal continuity of old forests has led to loss of sensitive species closely associated with such habitats because there was insufficient time or lack of sources for recolonization.

Lichens also are identified that indicate forest stand temporal continuity in northern boreal forests (Esseen and others 1996, Nilsson and others 1995, Selva 1994). Pike and others (1975) identify epiphytic lichens and bryophytes associated with old-growth forests of western Oregon. Söderström and Jonsson (1992) identify bryophytes that indicate fragmentation of old forests; that is, loss of old-growth bryophyte species in the more isolated forest fragments. In the current study, we identified 15 lichen groups and 9 bryophyte groups that may indicate old-growth forest conditions in the basin assessment area (see appendices B and C). The rotten log and tree base lichen group in particular indicates ecological continuity of old growth.

Many of the bioindicator species and groups identified here, including those of old-growth forests, can be useful to managers interested in quickly surveying potential environmental conditions without investing in long-term ecological research studies. Such indicators can serve to track effects of alternative management activities, such as variations in grazing, timber harvesting, or restoration regimes.

Invertebrates

Number of species—In the basin assessment area, some 24,270 species of macroinvertebrates are estimated to exist (Marcot and others 1997). This figure extrapolates for species not yet discovered in the basin assessment area and some not yet described, and comprises about 770 mollusks (425 freshwater gastropods, 35 freshwater bivalves, 30 slugs, and 280 land snails; T. Frest in Marcot and others 1997) and 23,500 arthropods, including insects. At present, only 3,780 species of macroinvertebrates (16 percent of all estimated species) have actually been reported from the basin assessment area, including 380 mollusks (200 freshwater gastropods, 30 freshwater bivalves, 25 slugs, and 125 land snails; T. Frest in Marcot and others 1997) (49 percent of all estimated mollusks) and 3,400 arthropods (14 percent of all estimated arthropods). An additional, large set of micro-organisms, including bacteria, protozoa, rotifers, viruses, and other taxa, occur. They may number in the hundreds of thousands of species but are mostly unknown and are treated here only by taxonomic groups.
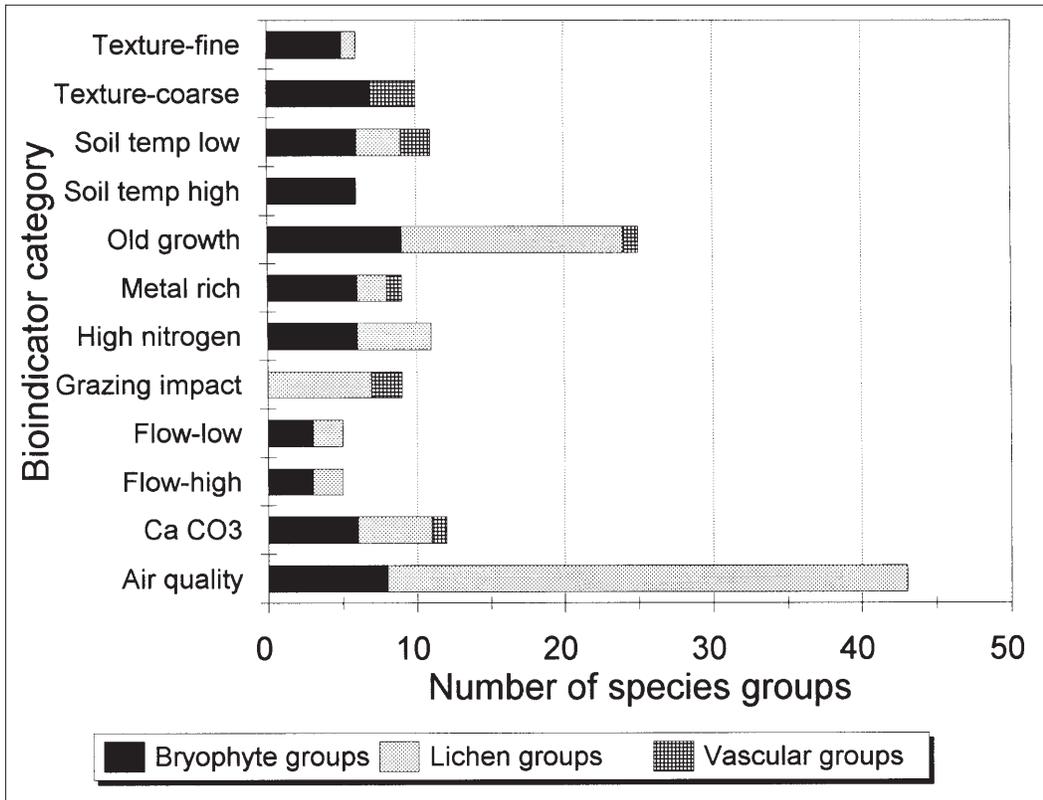
Figure 22—Number of lichen, bryophyte, and vascular plant species groups by bioindicator category. See appendices B and C for lists of groups, and text for explanation of categories.

The SER database lists only a small example set of 346 invertebrate species. Of these, environmental correlates and ecological functions are denoted for 195 individual species of arthropods and 11 species groups of micro-organisms (6 species groups of soil bacteria, 1 group of soil protozoa, 1 group of soil rotifers, and 3 groups of soil nematodes). Thus, the analyses that follow provide only examples of invertebrate species and micro-organism groups.

Dispersal modes and KEFs—Even for the relatively tiny set of example species explicitly included in this assessment, various dispersal modes and related KEFs were identified. Dispersal modes included various forms of independent locomotion (crawling and other flightless terrestrial movement), sedentary habits, soil digging, aerial movement (flying, ballooning, and drifting), budding, and phoresis (dispersal using other host species).

Phoretic dispersal exemplifies some interesting relations that have evolved among species. Phoretic dispersal has appeared in many micro-organisms and invertebrates, including bacteria, rotifers, protozoa, nematodes, and insects (table 7). Host species can include seeds, plants, organic debris, other insects, birds, mammals, and even humans. Soil bacteria are ubiquitous and disperse by means of most of these hosts. Rotifers and soil protozoa can hitch rides on arthropods, small mammals, birds, and even soil nematodes. Bacterial-feeding soil nematodes in turn can travel by arthropods, birds, small mammals, and even by humans via tools that redistribute soil, such as shovels.

Table 7—Examples of micro-organisms and invertebrates that disperse by phoresis (facultative associations among species, such as being carried and dispersed by other organisms)

Scientific name or general species group	Common name or specific species group	Dispersal mode	Dispersal requirements
Bacteria:			
Erwinia cartovora	Bacterial pathogens	Carried by seeds, plant debris, or alternative hosts, birds, or humans	Presence of bacterium in diseased plant or animal material; dispersal agent often required to move the pathogen from diseased host to susceptible host
Microcoleus	Beneficial bacteria	Phoretic on arthropods or small mammals and birds	Presence of the bacterial/lichens in undisturbed soil; feeding by dispersal agent
Bacillus thermophilus	Competitive bacteria	Phoretic on arthropods or small mammals or birds, or by inoculation	Presence of bacterium in undisturbed soil; feeding by dispersal agent
Pseudomonas fluorescens	Competitive bacteria in the rhizosphere	Phoretic on arthropods or small mammals or birds, or by inoculation	Presence of bacterium in undisturbed soil; feeding by dispersal agent
Klebsiella planticola	Bacteria: N-immobilizers	Phoretic on arthropods or small mammals or birds, or by inoculation	Presence of bacterium in undisturbed soil; feeding by dispersal agent
Rhizobium melliotii	Bacteria	Phoretic on arthropods or small mammals or birds, or by inoculation	Presence of bacterium in undisturbed soil; feeding by dispersal agent
Rotifers:			
Rotifers	Rotifers: no info about rotifer spp. in basin	Phoretic on arthropods, small mammals, birds, or nematodes	Presence in undisturbed soil; presence of dispersal agent
Protozoa:			
Amoeba amoeba	Protozoa: bacterial-predators	Phoretic on arthropods, small mammals, birds, or nematodes	Presence in undisturbed soil; presence of dispersal agent
Nematodes:			
Acrobeloides	Bacterial-feeding nematodes	Phoretic on arthropods, small mammals, or birds	Presence in undisturbed soil; presence of dispersal agent
Aphelenchus avenae	Fungal-feeding nematodes	Phoretic on arthropods, small mammals, or birds	Presence in undisturbed soil; presence of dispersal agent
Pratylenchus penetrans	Plant-feeding nematodes	Phoretic on arthropods, small mammals, birds, or human tools (shovel)	Presence of undisturbed soil; presence of dispersal agent

Table 7—Examples of micro-organisms and invertebrates that disperse by phoresis (facultative associations among species, such as being carried and dispersed by other organisms) (continued)

Scientific name or general species group	Common name or specific species group	Dispersal mode	Dispersal requirements
Fungi-related:			
Hysterangium	Ectomycorrhizal mat-forming fungi	Carried by nematodes, arthropods, or small mammals	Dispersal agents
Rhizoctonia solani	Fungal pathogens	Carried by seeds, plant debris, or alternative hosts, birds, or humans	Presence of bacterium in undisturbed soil; feeding by dispersal agent
Glomus mossae	Vesicular fungi	Carried by seeds, plant debris, arthropods, ants, or wind	Dispersal agents
Penicillium citrinum	Saprophytic fungi	Phoretic on arthropods, small mammals, birds, or by inoculation	Presence of bacterium in undisturbed soil; feeding by dispersal agent
Insecta:			
Cimex latipennis	Bed bug (Cimicidae: Hemiptera)	Flightless—disperse only on host animal	Presence of bats when proper life stages of bug available

Phoretic invertebrates play various roles in contributing to trophic structures and ecological processes of ecosystems. Many phoretic invertebrates consume soil micro-organisms and are prey for other consumers; they aid soil nitrogen cycling through nitrogen immobilization and by acting as a source for nitrogen mineralization, which can be vital functions in forest nitrogen conservation (Davidson and others 1992, Miller and others 1989). A few phoretic invertebrates are parasites or pathogens, or cause disease. Phoretic invertebrates also include soil-oriented species whose functions aid soil structure, enhance soil stabilization, detoxify xenobiotics, sequester (accumulate) soil metals, and influence vegetation succession and presence and diversity of plant species.

The SER database afforded the opportunity to explore some examples of how dispersal modes of invertebrates relate to their KEFs. Invertebrates with independent locomotion provide many ecological services in their ecosystems. Most of these example species included in the SER database were insectivorous and provide food for other insectivores, with a few being carrion feeders, detrivorous, or herbivorous on trees or shrubs, or feeding in water on algae or plankton. The four sedentary species were folivores.

Species dispersing by digging enhance the physical structure of soil and turnover of soil nutrients and layers. Earthworms are a prime example (see discussion in Marcot and others 1997). In one study of eight species of earthworms in a Kansas tallgrass prairie, James (1991) reported that total annual soil consumption by all earthworms was 4 to 10 percent of organic matter in the top 15 cm; 100 to 300 percent of plant annual belowground production passed through the earthworms each year; and mineral nitrogen processed was 10 to 12 percent of annual plant nitrogen uptake, comparable to half of the input from precipitation, whereas the phosphorus processed was equivalent to 50 percent of annual uptake. Native and introduced earthworm species, however, do not necessarily perform the same functions. James found that exotic, introduced earthworm species have a negative effect on soil turnover and nutrient mineralization because of the lower soil throughout and their relative intolerance of summer soil temperatures, as compared with the native earthworms.

Invertebrate species that disperse by flying, ballooning, or drifting cover an even wider array of trophic functions than those with independent locomotion, and include folivores, spermivores, sap feeders, root feeders, insectivores, soil micro-organism feeders, carrion feeders, aquatic herbivores, detritovores, and moss feeders. Many of these aerial-dispersing species (many Hymenoptera) serve as important pollination vectors critical for reproduction of flowering plants. They also include forest beetles, some of which can change the structure of terrestrial and aquatic habitats by causing tree mortality, breaking down standing dead trees and large down logs, creating canopy gaps in forest stands, and causing increased streamflow. Thus, providing suitable conditions and means of dispersal for invertebrates also provides for many ecological processes and species functions in the ecosystem.

Disease and parasites—The ecology of disease and parasites is not well studied in the basin assessment area and is poorly represented in the SER database. Disease can strongly mediate biodiversity and viability of many kinds of wild plants and animals and needs to be considered in wildlife conservation biology programs (Dobson and Mat 1986, May 1988, Scott 1988). Aguirre and Starkey (1994) conclude that proximity of domestic ungulates to wild ungulates can transmit disease and parasites and complicate wild ungulate management; they cite several examples, including bovine brucellosis (*Brucella abortus*) in bison (*Bison bison*) and Rocky Mountain elk in Yellowstone National Park, and lungworm (*Pasteurella* spp.)-pneumonia complex in bighorn sheep (*Ovis canadensis*) in several Western national parks (also see Peterson 1991). Simonetti (1995) cites other similar examples, and Cunningham (1996) warns of secondary transmission of parasite pathogens to wildlife during translocation projects. Disease transmission can exacerbate recovery of endangered species (Thorne and Williams 1988) and is a controversial facet of wild game ranching. Certainly, too, human health concerns warrant attention to wild pathogens, such as transmission of lyme disease by ticks (*Ixodes scapularis*) throughout the basin assessment area (Ostfeld and others 1995).

Parasites, however, also play ecological roles in ecosystems and serve as an ecological "glue" to bind many species' relations. Windsor (1995,

1996) provides many fascinating examples of this, including the following. Hybrid cottonwoods (*Populus fremontii* x *P. angustifolia*) are more susceptible to aphid parasites than are their parent species. Thus, aphids concentrate in the hybrid zone between the parents. This aphid sink discourages aphids from adapting to the more numerous parents, and it keeps the parents as separate species. Peterson (1991) calls for controlled experiments, or at least an adaptive management approach (learning by trial), to provide a sounder scientific basis for management of parasite-host interactions.

Many invertebrate parasite-host relations await discovery. For example, Boonstra and others (1980) found that botfly parasitism can affect vole populations. Dobson (1988) suggests that parasites can be used as an effective conservation biology weapon to control introduced mammals threatening fragile isolated or island biota.

Vertebrates

Number of species—In the basin assessment area, 468 species of vertebrates (excluding fish) are both estimated and known to exist (Marcot and others 1997). These include 26 species of amphibians, 27 reptiles, 283 birds, and 132 mammals. An additional 79 bird species are accidental or casual species in the basin assessment area.

The SER database lists 476 species of vertebrates, consisting of all the known species and including 291 species of birds (excluding the accidentals or casuals, but including 8 bird species that likely occur only sporadically in the basin assessment area). Thus, the analyses that follow provide a full accounting of all regularly occurring vertebrate species.

Endemic species—Findings on vertebrate species endemism within the basin assessment area are presented in Marcot and others (1997). To recap, two amphibian species are local endemics: Idaho giant salamander (*Dicamptodon aterrimus*) and Larch Mountain salamander (*Plethodon larselli*); and seven other amphibian species are regional endemics: northwestern salamander (*Ambystoma gracile*), Cope's giant salamander (*Dicamptodon copei*), Dunn's salamander (*Plethodon dunni*), Coeur d'Alene salamander (*P. idahoensis*), Cascade torrent salamander (*Rhyacotriton cascadae*),

red-legged frog (*Rana a. aurora*), and Cascades frog (*R. cascadae*). The locally endemic amphibian species occur in 9 vegetation cover types, and the regionally endemic species occur in 20. Locally or regionally endemic amphibians are particularly rich (more than six species) in several montane forest vegetation cover types, including Pacific silver fir/mountain hemlock forest, mountain hemlock forest, interior Douglas-fir forest, and western redcedar/western hemlock forest. Other vegetation types, however, also may be necessary to ensure the long-term persistence and distribution of some of these species.

No reptile was determined to be locally endemic or regionally endemic. Many reptile species occur only along the margins of the basin assessment area and beyond, such as in the Great Basin and Klamath Basin to the south.

There are no locally endemic birds, and four are regionally endemic: sage grouse (*Centrocercus urophasianus*), rufous hummingbird (*Selasphorus rufus*), northern spotted owl (*Strix occidentalis caurina*), and Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*). Collectively, these taxa occur widely throughout most vegetation cover types, although specific ranges of some of these taxa (especially Columbian sharp-tailed grouse) are quite limited within the basin assessment area.

Among mammals, local endemics include two species (Idaho ground squirrel (*Spermophilus brunneus*) and Washington ground squirrel (*S. washingtoni*)) and two subspecies (potholes meadow vole (*Microtus pennsylvanicus kincaidi*) and White Salmon pocket gopher (*Thomomys talpoides limosus*)). There may be other locally endemic subspecies of mammals not recognized in this study. Some 22 other mammal species are regional endemics (see Marcot and others 1997 for list). Collectively, local endemics and regional endemics occur widely throughout most vegetation cover types of the basin assessment area but are concentrated somewhat more in drier forest, shrub, and herb communities. Vegetation cover types that are particularly rich in locally or regionally endemic mammals (>12 species) include mixed-conifer woodland, big sagebrush (*Artemisia vaseyana*), native forb, mountain big sagebrush, and low sage. High numbers of endemics occur in mixed-conifer forests probably
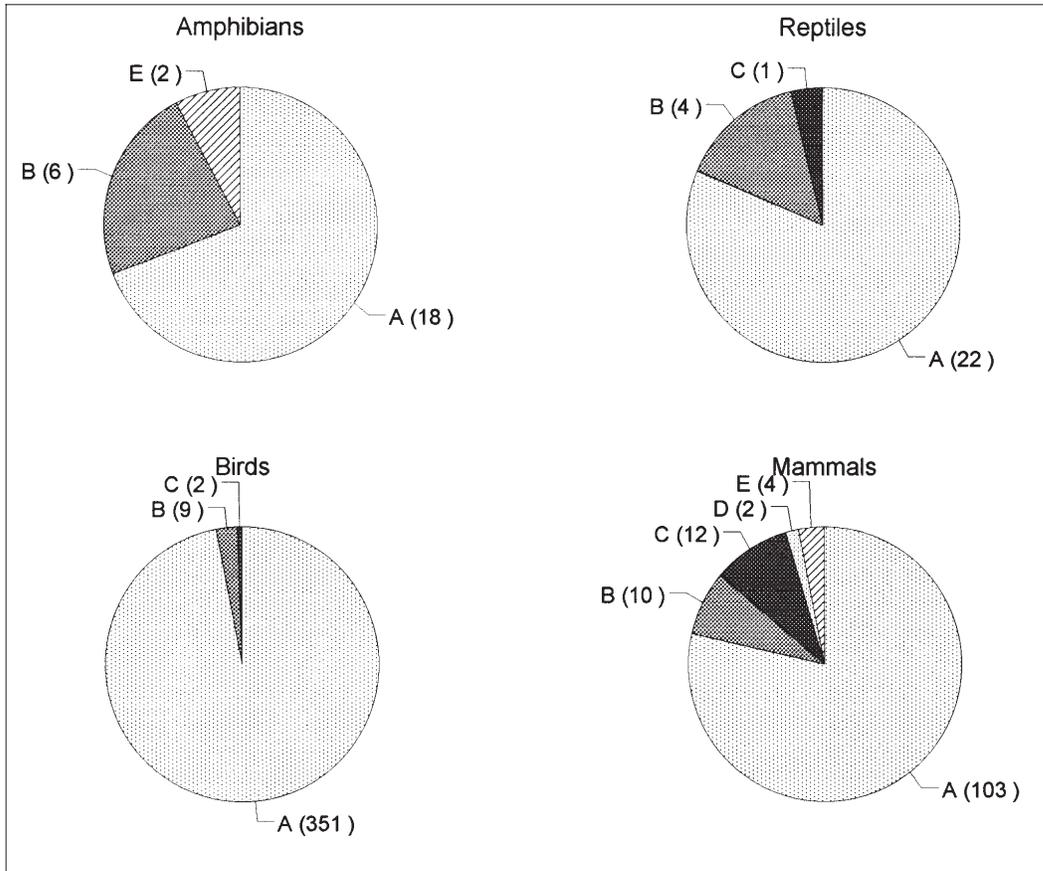
Figure 23—Number of vertebrate species by taxonomic class, by proportion of species' range lying outside the basin assessment area. Species range categories: A = nearly all (80 to 99 percent) of the overall species range occurs outside the assessment area; B = more than half, but not nearly all (60 to 79 percent) occurs outside; C = about half (40 to 59 percent) lies outside; D = less than half, but not only a very small portion (20 to 39 percent) lies outside; and E = only a very small portion (0 to 19 percent) lies outside.

because such forests occupy a wide range of moisture and temperature conditions and their overall species diversity is typically high (Harvey and others 1989, Sayler and Martin 1996).

The number of species that are local and regional endemics among amphibians, reptiles, birds, and mammals was not significantly different than the number of all nonendemic vertebrates by taxonomic class. That is, local and regional endemics were not more apt to be of any particular vertebrate class (Marcot and others 1997).

Species by percentage of range within the basin assessment area—A complementary way of considering patterns of endemism is the percentage of a species' range that lies beyond the basin assessment area. We identified five categories for percentage of range: (A) nearly all

(>79 percent) of the species' range lies beyond the basin assessment area; (B) more than half but not nearly all (70 to 79 percent) lies beyond; (C) about half (69 to 40 percent) lies beyond; (D) less than half (20 to 39 percent) lies beyond; and (E) only a very small portion (<20 percent) lies beyond.

By taxonomic class, about two-thirds of the amphibian species have more than half their ranges beyond the basin assessment area (range categories A and B); only two amphibian species (the two local endemics) are locally confined (range category E) (fig. 23). Reptiles and birds are even more broadly distributed. Among mammals, about 95 percent of the species have half or more of their range beyond the basin assessment area (range categories A, B, and C); and only six taxa

have their range mostly or entirely within the basin assessment area (range category E). These six mammal taxa include all four local endemics plus two other sciurids: Uinta ground squirrel (*Spermophilus armatus*) and red-tailed chipmunk (*Tamias ruficaudus*).

Species that migrate and spend part of their year elsewhere but that restrict their distribution during one part of the year to a specific region (such as the basin assessment area), are called **semiendemic species** by Garza (1996). Semiendemics can include Neotropical migratory birds and other species that occur only seasonally in a given region. Garza argues that species that are confined to a specific geographic region, even if only for a portion of the year, still should be considered as restricted to that area for purposes of habitat conservation. Because our range maps show neither season of use nor migration range beyond the basin assessment area, our designation of migratory species into endemism and percentage of range classes approximates the concept of semiendemics. Thus, some migratory species might occur as semiendemics in the basin assessment area but rank only as range categories A, B, or C.

Another way of looking at abundance patterns among range classes is shown in figure 24. Most species that extend beyond the basin assessment area (range categories A, B, and C) are birds and mammals, with a smaller proportion of amphibians and reptiles. Those somewhat more confined to the basin assessment area (range category D) are all mammals, and those most confined to the basin assessment area (range category E) are amphibians and small mammals.

We were surprised to find so few vertebrates, especially species with small body size, to be local or regional endemics, and so few vertebrates with ranges mostly confined to the basin assessment area. It is evident that the administrative and hydrologic boundaries of the basin assessment area do not particularly circumscribe unique vertebrate communities and species ranges. This is because the basin assessment area is "land-locked," and much of its ecological character along the margin spills into adjacent areas, including the western slope of the Cascade Range in western Washington and Oregon, the Klamath Basin and Great Basin in northern California and Nevada, the

Greater Yellowstone Ecosystem in Wyoming, the northern glaciated mountains in the Canadian Rocky Mountains, and the Okanogan Highlands in the Okanagan[6] Desert of British Columbia, Canada. Marcot and others (1997) list vertebrate species closely associated with many ERUs, and many of these assemblages consist of species that range well beyond the basin assessment area in many of these directions.

Abundance, breeding status, and migration status of birds—Abundance, breeding status, and migration status of birds in particular were categorized by state and for the entire basin assessment area. The total number of birds (including accidentals and casuals) occurring by state was remarkably constant, ranging between only 360 and 362 species. The total number of breeding birds (migrants plus residents) by state averaged 221 species and ranged from 192 species in Wyoming to 242 species in Oregon. (It should be remembered that these species tallies refer only to those portions of these states that lie within the basin assessment area.) This breeding-bird richness is quite close to that suggested by Huston's (1994:25) plot of latitudinal gradient in species richness of breeding birds in North and Central America. The basin assessment area lies between latitude 42º and 49º N., for which Huston's bird species richness curve predicts about 200 species (but the data scatter on the curve suggests upward of 300 species empirically).

For the basin assessment area as a whole, most bird species were ranked as common, with fewer species uncommon or rare, fewer still as abundant, and the fewest as irregular (fig. 25).[7] This general bird abundance pattern also held for most of the five western states included in this part of the assessment (Washington, Oregon, Idaho,

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[6] A word on spelling: the United States has the Okanogan Highlands and Canada has the Okanagan Desert, but they do constitute a single shared ecosystem.

[7] If the abundance categories can be taken as approximate octaves or geometric series, then the bird species abundance histograms match well those reported in other north temperate ecosystems, such as nesting bird species in Quaker Run Valley, New York (Krebs 1978:452). Such species abundance patterns are somewhat stable attributes of continental communities.
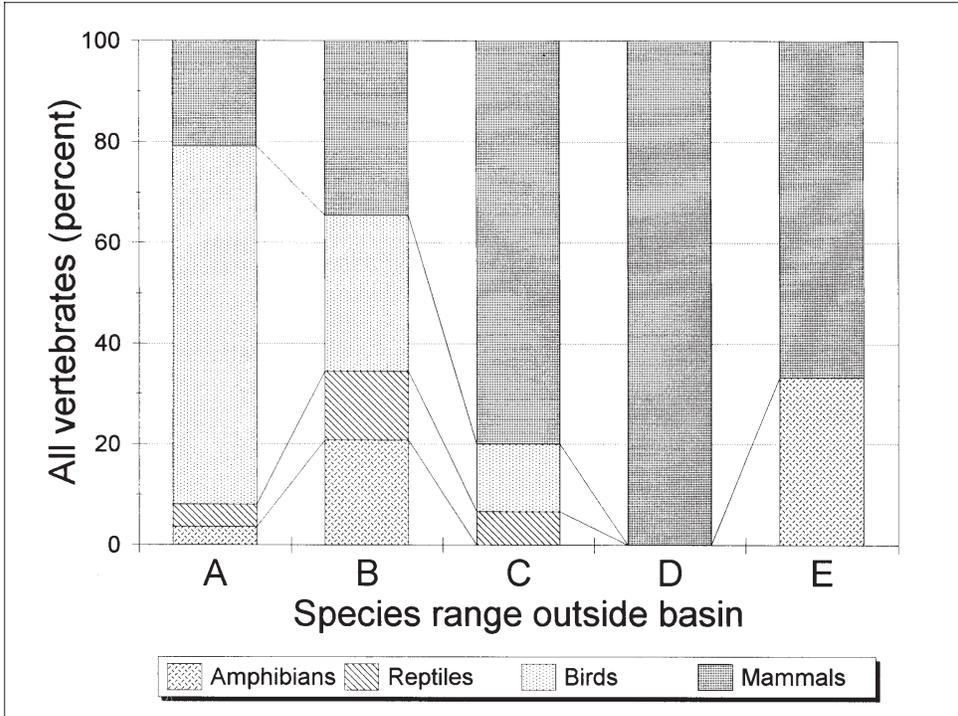
Figure 24—Percentage of all vertebrate species by taxonomic class, showing proportion of species' range lying outside the basin assessment area (see fig. 23 for description of species range categories).
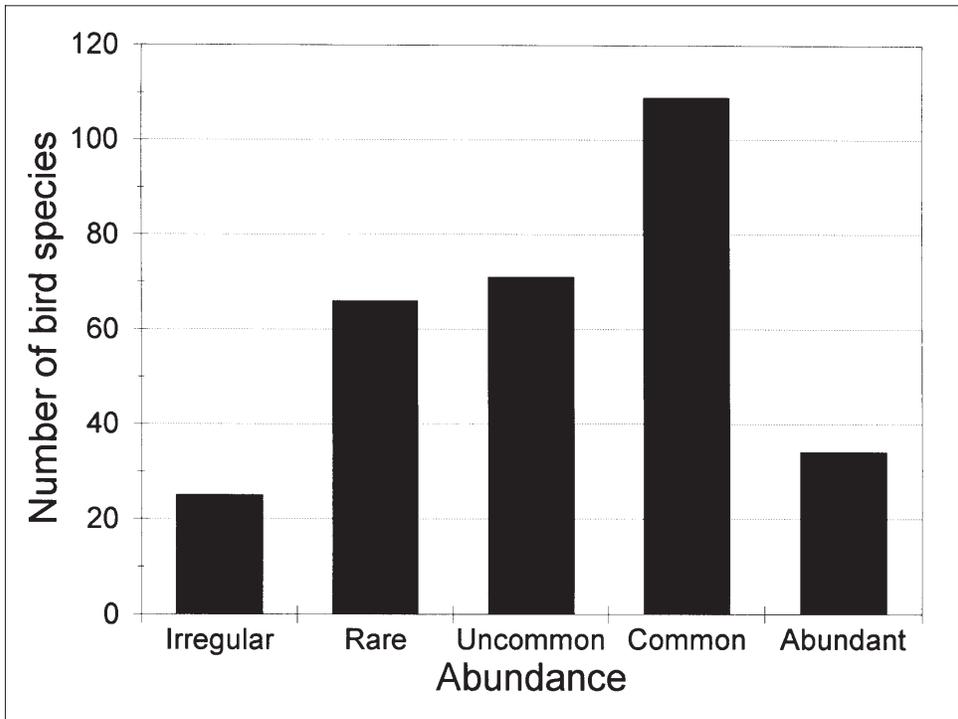

Figure 25—Number of bird species by abundance category (see text for definitions of categories).

Montana, and Wyoming; data for Nevada and Utah were not available for those small portions present in the basin assessment area), with a few deviations (fig. 26). Most of the irregular species occur in western Montana, which is located toward midcontinent and which picks up many species found more commonly in other, adjacent continental ecosystems. Examples of irregular species in western Montana are McCown's longspur (*Calcarius mccownii*), which is more of a prairie species farther east, black-throated blue warbler (*Dendroica caerulescens*), which occurs more commonly in Eastern U.S. states, and hoary redpoll (*Carduelis hornemanni*), which is an irregularly irruptive species from northern latitude boreal and subboreal forests. On the other hand, likely for the same reasons of being more central in the continent, western Montana has the greatest number of abundant species, and northwestern Wyoming has the greatest number of common species in the basin assessment area (fig. 26).

As for breeding and migration status of birds throughout the basin assessment area, most species are resident (36 percent) or summer breeders (26 percent), with fewer species occurring as migrants (14 percent), winter only (7 percent), or nonbreeding summer residents (2 percent) (the remaining 15 percent were not specified) (fig. 27). Proportions of bird species in these breeding and migration classes generally were consistent across the states but with a decreasing proportion of residents and increasing proportion of migrants toward midcontinent (fig. 28).

Tallying number of bird species by abundance status and by breeding and migration status revealed interesting geographic trends by state (fig. 29). Throughout the five states included in this part of the analysis, most of the abundant, common, and uncommon bird species were residents and summer breeders. Far fewer abundant bird species occurred in Idaho and Wyoming than in the other three states. Rare bird species included various mixes of breeding status categories by state with no clear geographic pattern,

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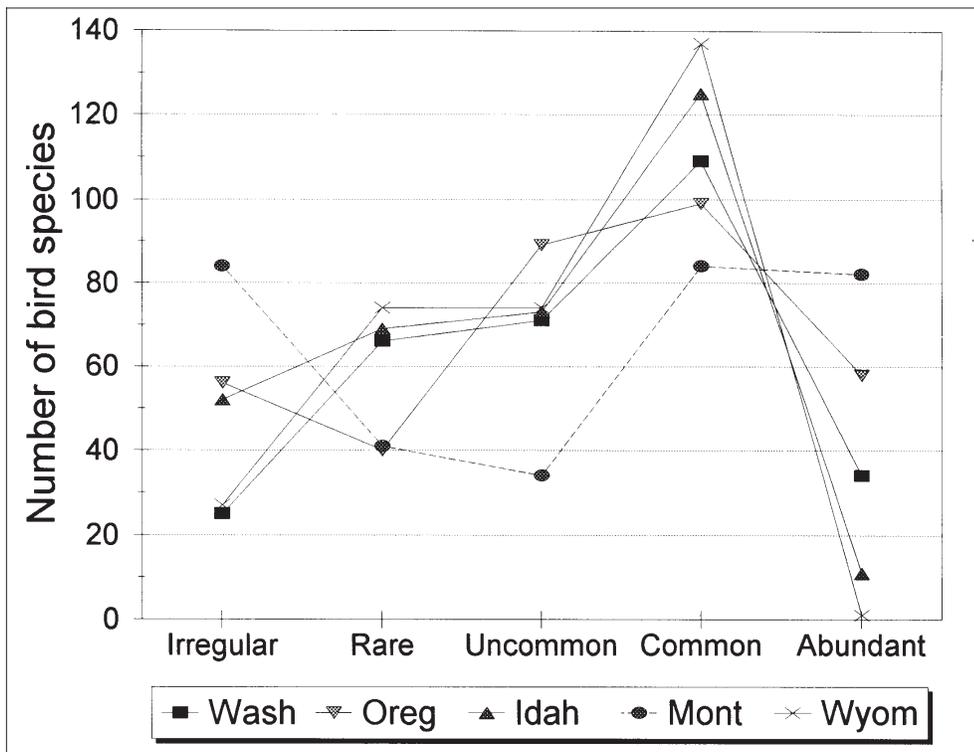
Figure 26—Number of bird species by abundance category and U.S. state, within the basin assessment area (see text for definitions of categories).
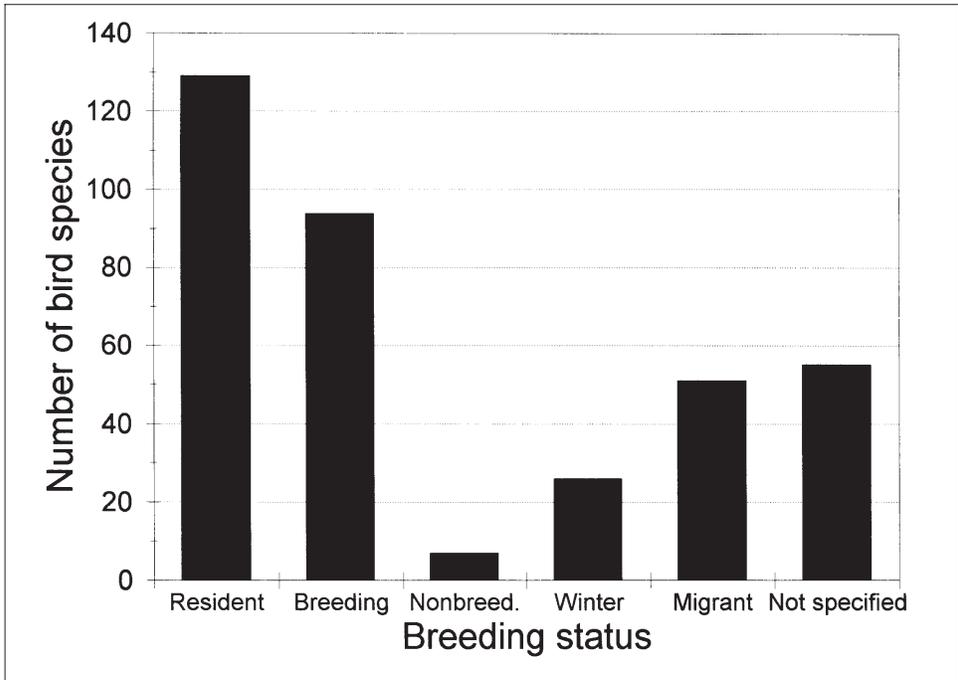
Figure 27—Number of bird species by breeding status category, within the basin assessment area (see text for definitions of categories).
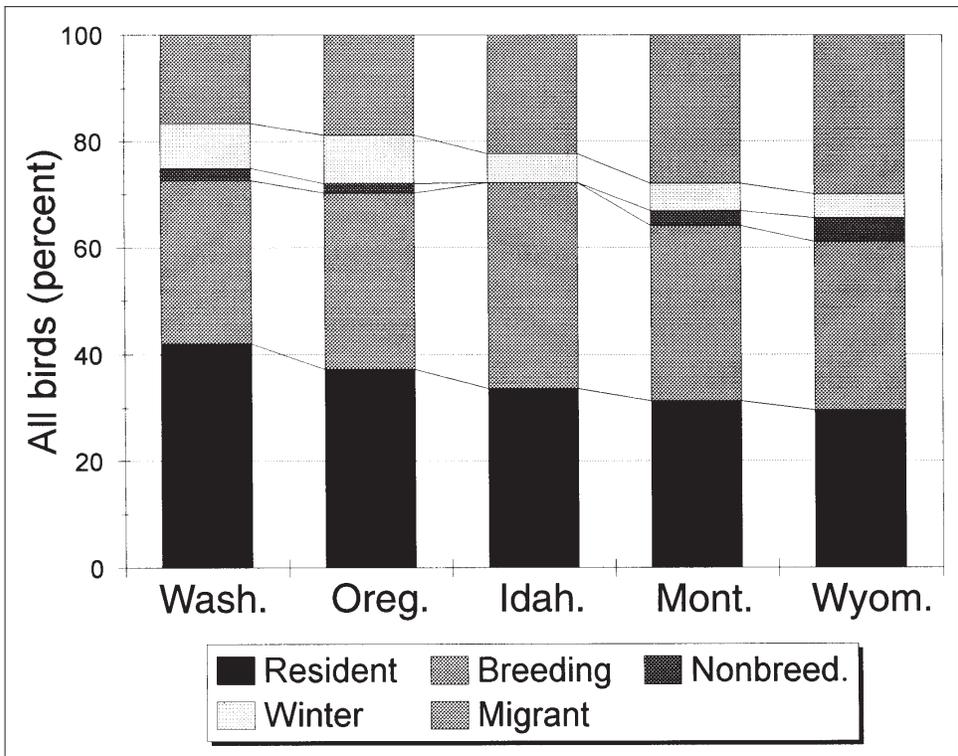
Figure 28—Percentage of bird species listed by breeding status category and U.S. state, within the basin assessment area (see text for definitions of categories).
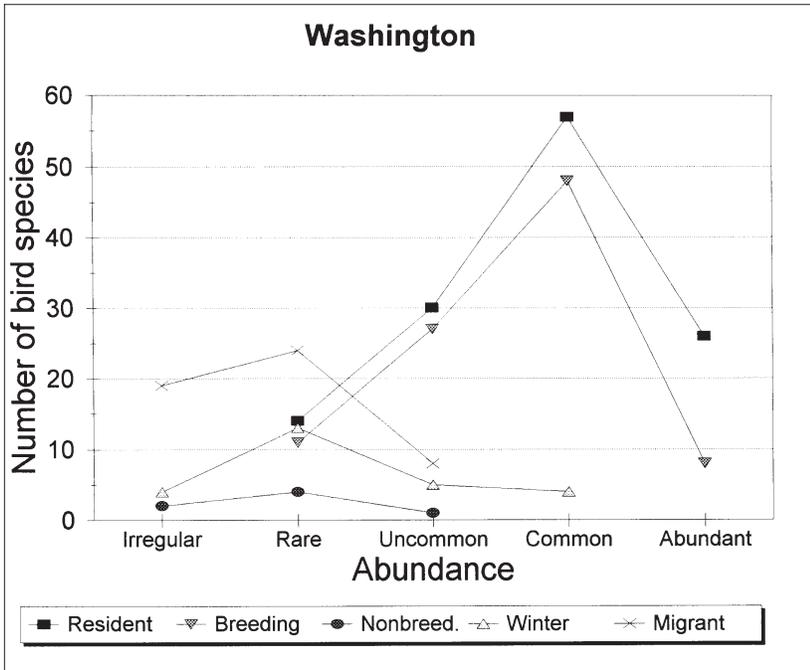
Figure 29—Number of bird species listed by abundance category, breeding status category, and U.S. state, within the basin assessment area (see text for definitions of categories).

Figure 29—continued

Idaho

Figure 29—continued

Montana
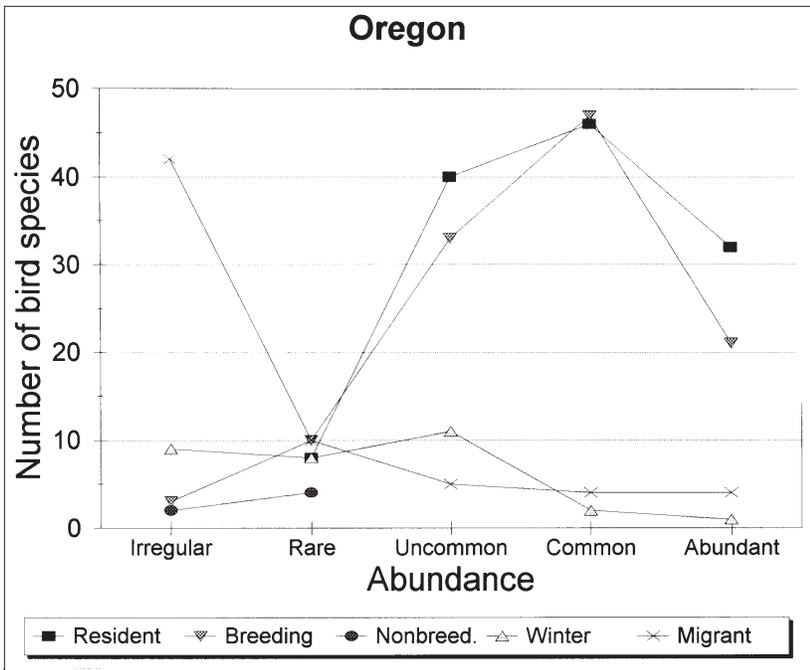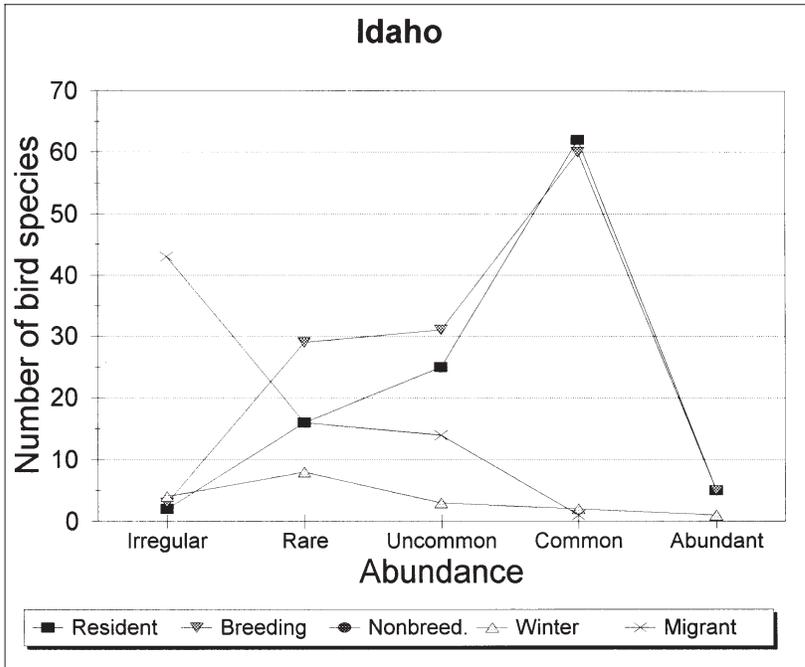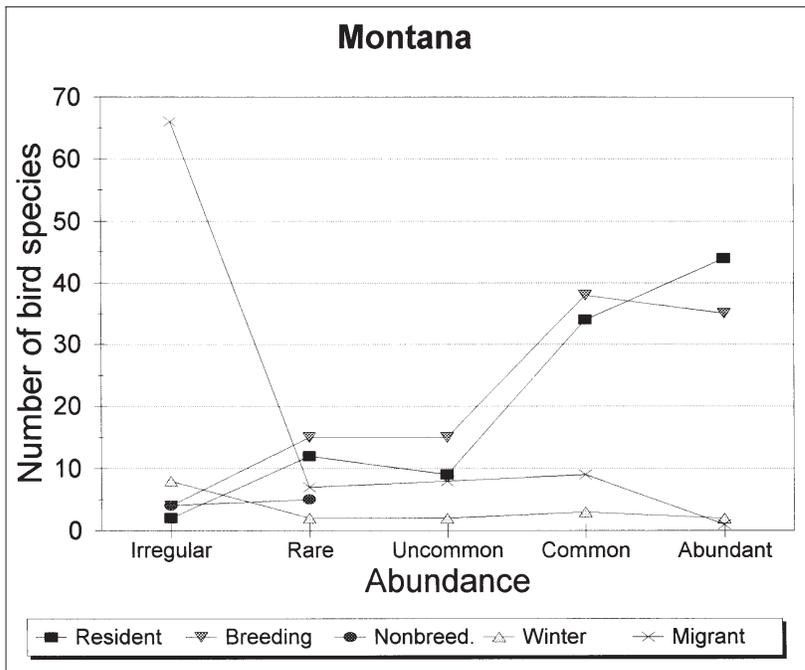
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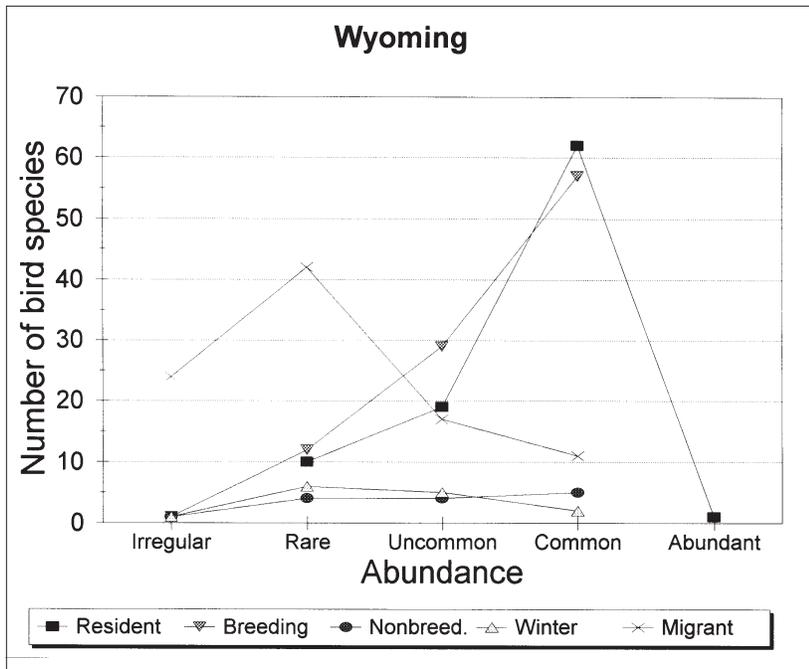
Wyoming

Figure 29—continued

although Wyoming and Washington had more rare migrants than did other states. Among all five states, irregular species consistently comprised mostly migrants. Because of their geographic mobility, migrants, especially long-distance migrants, are more apt to appear irregularly in individual states than are birds of other breeding status categories.

Brood parasitism—Among vertebrate parasites, brown-headed cowbirds (*Molothrus ater*) are nest parasites of Neotropical migratory songbirds and are a factor in their decline (Brittingham and Tempe 1983, Rothstein and others 1980; see Marcot and others 1997 for a list of host species of the basin assessment area). Not all hosts may respond the same, however. Uyehera and Narins (1995) experimentally demonstrate that willow flycatchers (*Empidonax traillii*) can differentially recognize female and male cowbirds near their nests, and that the behavior of the flycatchers acts as a counteradaptation to thwart brood parasitism.

Species function profiles—Numbers of species with selected KEFs were tallied by terrestrial vegetation community. We term these depictions "species function profiles" (fig. 30), which depict variations in functional redundancy among ter-

restrial vegetation communities (table 2). For this analysis, we selected a range of KEFs that seemed particularly pertinent to vertebrates and for which variations in numbers of vertebrate species among communities might prove instructive (table 8).

We explored patterns of two trophic relations functions. The first was presence of heterotrophs (table 8), which can include primary consumers or herbivores, secondary consumers or primary predators, tertiary consumers or secondary predators, omnivores, carrion feeders, cannibals, and coprovores (feed on fecal material). As expected, the number of vertebrate heterotroph species did not differ significantly among terrestrial vegetation communities (fig. 31a) because heterotrophy is a generalized function of all vertebrate species (380).

We then narrowed the focus to carrion feeders, which include at least seven species: Great Basin spadefoot (*Spea intermontana*), which also feeds on insects, small invertebrates, and sometimes each other (cannibalism); coyote (*Canis latrans*), an opportunist scavenger for which carrion is most important during winter; wolverine (*Gulo gulo*); turkey vulture (*Cathartes aura*), whose feeding behavior significantly contributes to decomposition of carcasses; bald eagle (*Haliaeetus*
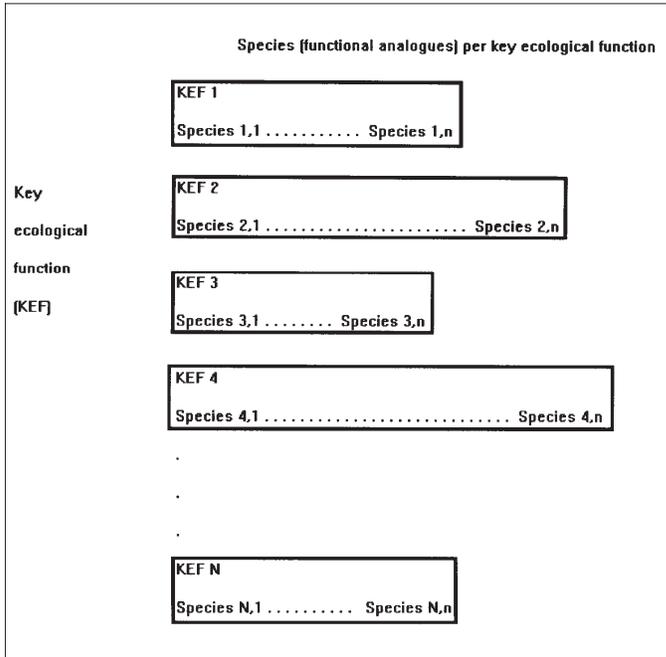
Figure 30—The general form of species function profiles showing functional redundancy and total species functional diversity in a community. Each of the KEFs in a community has a number of species with that function. Species function profiles are graphs displaying the numbers of species with each specific KEF across communities. Functional redundancy is the number of species with a specific KEF in a given community. Total species functional diversity is the number of KEFs times the mean number of species per KEF (adapted from Huston 1994:5).

Table 8—Codes used in the species function profiles (fig. 31) for key ecological functions (KEFs) of species[a]

KEF code	Description of KEF
1.2	Heterotrophic consumer (380)
1.2.5	Carrion feeder (7)
2.1	Ungulate herbivory (may influence rate or trajectory of vegetation succession and presence of plant species) (15)
3.1	Nutrient cycling relations: aids in physical transfer of substances for nutrient cycling (C,N,P, other) (32)
4.1	Interspecies relations: potential insect population control (22)
4.2	Interspecies relations: vertebrate population control (10)
4.3	Interspecies relations: pollination vector (6)
4.4	Interspecies relations: transportation of seed, spores, plant or animal disseminules (153)
4.8	Interspecies relations: primary cavity excavator in snags or live trees (17)
4.9	Interspecies relations: primary burrow excavator (fossorial) (39)
6.1	Soil relations: physically affects (improves) soil structure, aeration (typically by digging) (10; combined with KEF 6.2)
6.2	Soil relations: aids general turnover of soil nutrients and layers (10; combined with KEF 6.1)
7	Wood relations (breaks down wood) (4)

[a] Total number of vertebrate species with each KEF within the basin assessment area is shown in parentheses. Taken from a longer classification presented in Marcot and others (1997).
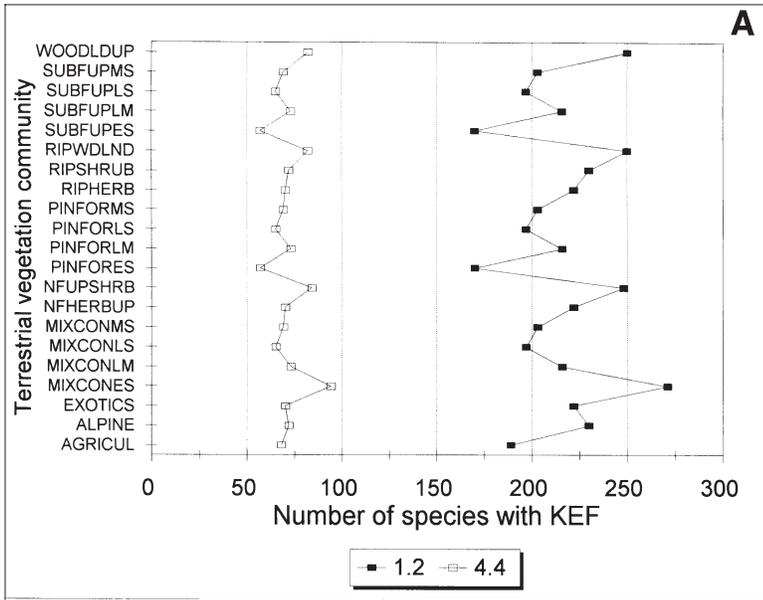
Figure 31—Vertebrate species function profiles. These show the number of vertebrate species that have specific KEFs, listed by terrestrial vegetation community, within the basin assessment area. See table 8 for description of KEFs. (A) KEF 1.2 = heterotrophic consumer, KEF 4.4 = transportation of plant or animal disseminules; (B) KEF 1.2.5 = carrion feeder, KEF 2.1 = herbivory; (C) KEF 3.1 = nutrient cycling, KEF 4.1 = potential insect control, KEF 4.2 = vertebrate population control; (D) KEF 4.3 = pollination vector, KEF 4.8 = primary cavity excavator; and (E) KEF 4.9 = primary burrow excavator, KEF 6.1 or 6.2 = soil structure relations, KEF 7 = wood relations (breaks down wood). Note that three terrestrial vegetation codes included in table 2 are not displayed here; these are urban, water, and rock-barren communities.

Figure 31—continued

Figure 31—continued

Figure 31—continued

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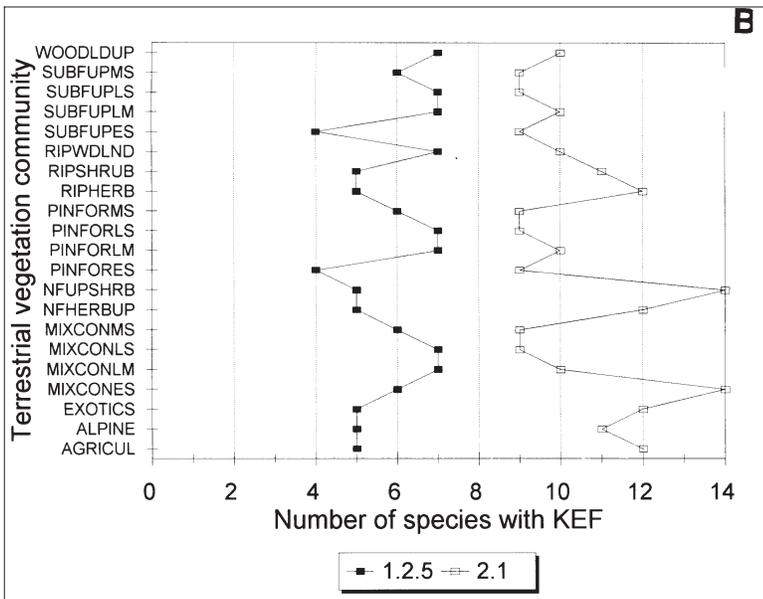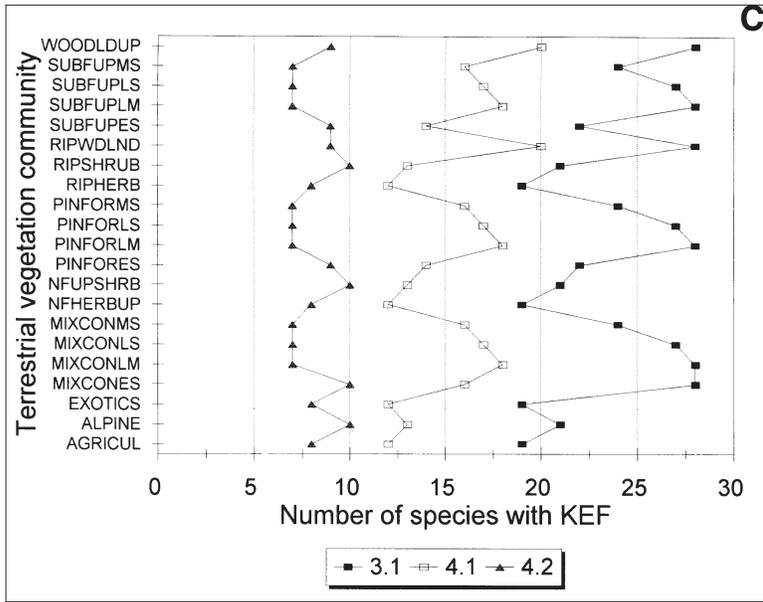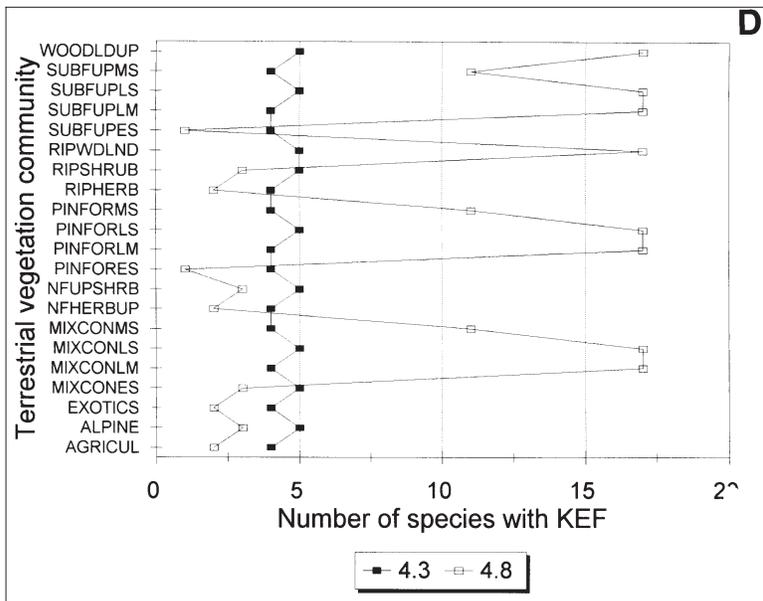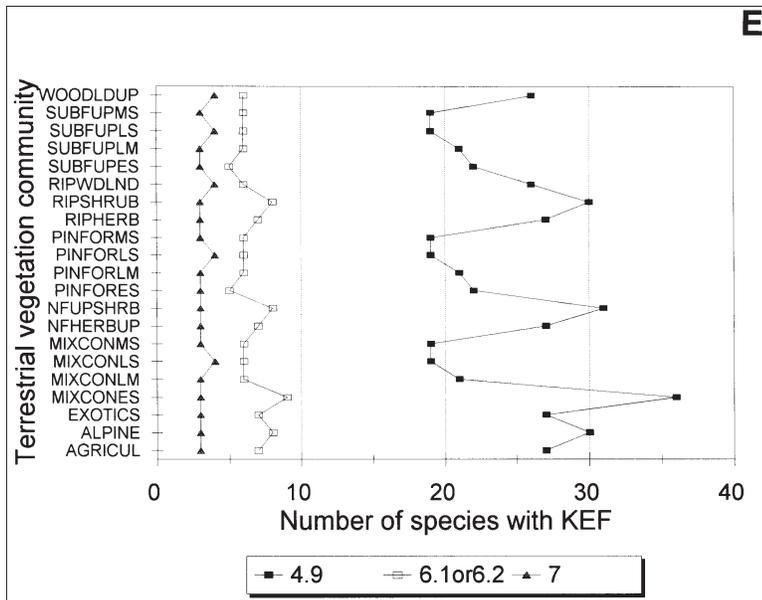
Figure 31—continued

leucocephalus), which can also take live prey; common raven (*Corvus corax*); and gray jay (*Perisoreus canadensis*), an omnivore. Other vertebrate species doubtless feed on carrion as well. Presence of the seven species listed here was more variable among terrestrial vegetation communities (fig. 31b) than was the general function of heterotrophy. The fewest number of carrion-feeders—that is, the least functional redundancy of the vertebrate community for this particular ecological function—occurred in early seral ponderosa pine forest and early seral subalpine forest vegetation communities, and reached its maximum in late seral forests and woodlands.

Herbivory is another subset of heterotrophy, and an ecological function that displayed a profile different from that of carrion feeding. Herbivory reached its greatest functional redundancy in early seral montane forest and in upland shrub vegetation communities (fig. 31b). As an ecological force, herbivory can alter the vegetation structure and succession of habitats. For example, moose (*Alces alces*) heavily browse early seral species such as aspen and willow, which can result in increases of conifers in habitats otherwise dominated by deciduous shrubs and trees (also see Pastor and others 1993). In semipalustrine habitats, plant communities can be altered by herbivory of several species of waterfowl, including greater white-fronted goose (*Anser albifrons*),

brant (*Branta bernicla*), snow goose (*Chen caerulescens*), and Ross' goose (*C. rossii*). Montane voles (*Microtus montanus*) and meadow voles (*M. pennsylvanicus*) can modify grassland structures through herbivory. Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Rocky Mountain elk (*Cervus elaphus nelsonii*), and mountain goat (*Oreamnos americanus*) can have major influences on composition and succession of vegetation through herbivory. Mountain goats can alter alpine and some subalpine plant communities. Herbivores can also interact with pollinators and affect plant reproduction and the evolution of plant traits (Brody 1996).

Another KEF is that of nutrient cycling relations, particularly species that substantially aid in physical transfer of substances for nutrient cycling. Essentially, all organisms cycle nutrients. At least some 32 vertebrate species, however, affect nutrient cycling substantially in their environments (see Marcot and others 1997 for discussion). The vertebrate species function profile for generalized nutrient cycling relations suggests a fair amount of variability of functional redundancy among communities (fig. 31c). Communities with the greatest redundancy in nutrient cycling functions among vertebrate species include late seral stages of most forest types, upland and riparian woodlands, and early seral montane forest. Com-

munities with the least redundancy include agricultural, alpine, exotic, upland herb and shrub, and riparian herb and shrub communities, possibly because of overall lower vertebrate species richness in at least some of these communities.

We developed species function profiles for six categories of interspecies relations: potential insect population control, vertebrate population control, pollination vectors, transportation of plant or animal disseminules, primary cavity excavation, and primary burrow excavation (fig. 31). Some 22 species of insectivorous amphibians, birds, and mammals have the potential for controlling some nonirruptive insect populations; some woodpeckers can dampen the amplitude of irruptive insect populations (Koplin 1969). Functional redundancy of potential insect control was greatest in upland and riparian woodlands and least in upland and riparian herbland, exotic, and agricultural communities.

Predatory activities of at least 10 species can control vertebrate populations. The species include five mammalian carnivore predators and two raptors. Examples include American kestrel (*Falco sparverius*), which may aid in population control of some insects and rodents, and American badger (*Taxidea taxus*), which may help control ground squirrel populations. Redundancy of vertebrate population control was less variable among communities but reached its peak in upland and riparian shrub, upland woodland, early seral montane forest, and—interestingly—alpine communities; and was least in most mid and late seral forest communities.

At least six birds—five hummingbirds and an oriole—serve as pollination vectors for flowering plants (see Marcot and others 1997 for discussion). This species assemblage did not show much variation in redundancy among vegetation communities (fig. 31d). Another, much larger set of 153 species serve to transport plant or animal disseminules; this set showed a fair amount of variation in redundancy among communities, with the greatest redundancy (most species) in early seral montane forest, upland shrub, riparian woodland, and upland woodland communities, and the least redundancy in early seral ponderosa pine forest and early seral subalpine forest (fig. 31a).

Primary cavity excavators—mostly woodpeckers, nuthatches, and chickadees—number 17 species (see Marcot and others 1997 for discussion) and showed by far the greatest variation in functional redundancy among vegetation communities of all ecological functions explored here (fig. 31d). Primary cavity excavation reached its greatest redundancy by far in all late seral forests and upland and riparian woodland communities; and its lowest redundancy in agricultural, alpine, exotics, upland and riparian herbland, upland and riparian shrubland, and early seral forest communities.

Primary burrow excavators, a set of 39 species (see Marcot and others 1997 for discussion), also showed significant variation among communities. The greatest functional redundancy was reached in early seral montane forest, upland and riparian shrub, and alpine communities, and the least functional redundancy was reached in late seral forest communities, a rather inverse pattern to that of primary cavity excavators (fig. 31e). As with invertebrate soil excavators, among vertebrates the primary burrow excavators can be important to soil turnover and mixing of organic matter. Gophers, for example, can process an enormous quantity of soil material. In one study in coastal San Diego County, California, Cox (1990) found that the total soil mined by pocket gophers (*Thomomys bottae*) in 10 Mima-type mounds amounted to 8.23 $Mg^{-1} \cdot ha^{-1} \cdot yr^{-1}$ and subsurface deposition was 20.31 $Mg^{-1} \cdot ha^{-1} \cdot yr^{-1}$, so that total soil mining equalled 28.54 $Mg^{-1} \cdot ha^{-1} \cdot yr^{-1}$.

Finally, soil relations and wood relations showed relatively little variation in functional redundancy among communities (fig. 31e). Soil relations functions showed the greatest redundancy in early seral montane forest, and upland and riparian shrub communities, and the least redundancy in early seral ponderosa pine forest and early seral subalpine forest communities.

What general trends can be summarized from the patterns of these selected ecological functions? First, no one vegetation community harbors the greatest redundancy of all ecological functions. Most vegetation communities contribute to greatest redundancy of some specific ecological function. Thus, collectively, all vegetation communities combined help provide for redundancy of all ecological functions. Exceptions seem to be

agricultural and exotic (and urban) communities, which typically provide poorly for most functions explored here.

As a corollary, late seral forest communities seem to provide the greatest redundancy in carrion feeding, general nutrient cycling, and primary cavity excavation functions. Late seral forest communities provide poorly for vertebrate population control and primary burrow excavation functions, which reach their peaks of redundancy in other communities, principally early seral forest communities.

Alpine communities provide for high redundancy in vertebrate population control and in primary burrow excavation functions. Out of six mammal species that regularly function as secondary burrow users (that is, use burrows created by primary burrow excavators), however, only two species (ermine [*Mustela erminea*] and long-tailed weasel [*M. frenata*]) occur in alpine communities, and these species occur widely throughout other vegetation communities as well. Thus, although alpine communities provide for high functional redundancy of primary burrow excavation, it does not provide for high redundancy of secondary burrow use.

Upland and riparian herblands do not provide for maximum redundancy of any of the functions explored here. Upland and riparian shrublands provide for high levels of redundancy of herbivory, vertebrate population control, pollination, primary burrow excavation, and soil-relations functions. Upland and riparian woodlands provide for high levels of redundancy of carrion feeding, general nutrient cycling, potential insect population control, vertebrate population control, pollination, and primary cavity-excavation functions. Thus, shrublands and woodlands provide for complementary sets of ecological functions, just as do late and early seral forest communities.

Early seral montane forest seems to provide for an anomalously wide array of conditions and ecological functions of all forest types in the basin assessment area. It provides for high redundancy of general nutrient cycling, vertebrate population control, pollination, primary burrow excavation, and soil-relations functions, whereas early seral ponderosa pine forest and early seral subalpine forest communities do not. This may have to do with the overall greater habitat and biotic diver-

sity found in early seral montane forests than in early seral stages of other forest types, but this needs verification.

Which KEFs considered here are the most variable among terrestrial vegetation communities in terms of number of vertebrate species (redundancy of species)? The answer is found by plotting the standard error (SE) of number of species among vegetation communities for each KEF. Results (fig. 32) show that, of the functions considered here, primary cavity excavation is by far the most variable in functional redundancy of species among all terrestrial vegetation communities. This means that only specific vegetation communities are likely to support most of the species with this function. The next two functions with high variation in redundancy are the carrion feeder function and the primary burrow excavator function. Thus, the vegetation communities in which these most-variable functions occur are likely to be important for maintaining these species' ecological functions within the basin assessment area. On the other hand, KEFs with the lowest SEs include transport of plant or animal disseminules, heterotrophic consumer, and pollination vector functions. These are the least variable in redundancy and the most reliable among communities; none of the vegetation communities is particularly critical for maintenance of these functions within the basin assessment area (although specific composition of species with these functions may differ among communities).

Which terrestrial vegetation communities are the most variable in terms of redundancy among ecological functions? The answer is found by plotting the SE of species richness (number of species) among KEFs for each vegetation community. Results (fig. 33) suggest that early seral montane forest has the greatest variation, and three communities (mid seral montane forest, mid seral ponderosa pine forest, and mid seral subalpine forest) have the least variation in redundancy among the ecological functions discussed above. This does not mean that low-variation vegetation communities contain all KEFs, but only that the functions they do provide for tend to vary the least in number of species per function; there is a greater "evenness" (relative proportion) but not necessarily "richness" (number of different kinds) of species' ecological functions.
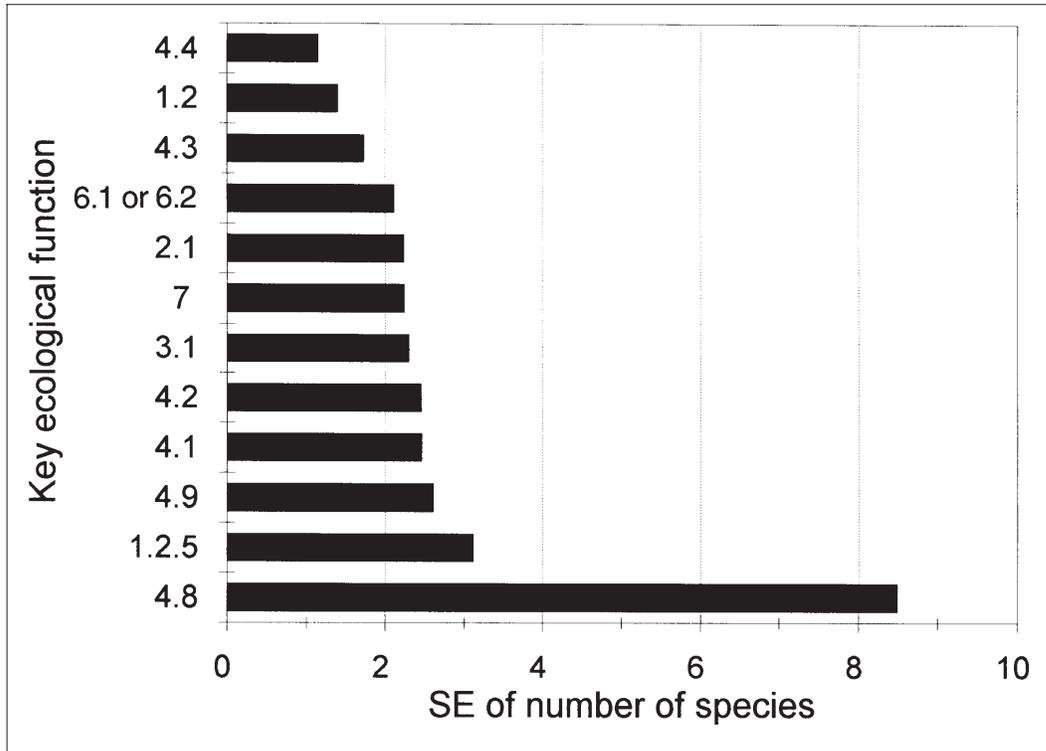
Figure 32—Variation in functional redundancy of KEFs among terrestrial vegetation communities, displaying SE of number of species among vegetation communities, by KEF. Greater SE values denote greater variation in functional redundancy among communities (see fig. 31 and table 8 for descriptions of KEF codes).

Overall, it is unclear how the degree of functional redundancy of KEFs, either among species or among vegetation communities, specifically affects long-term resiliency of ecosystems to perturbations of the environment and to perturbations of species community structures. A working hypothesis might suggest that a greater redundancy promotes greater resiliency in ecosystem ecological processes to stochastic environmental events and to short-term or localized losses of some species. This, however, is largely unstudied in the basin assessment area. Our approach provides an analytic framework and a repeatable means of posing such testable hypotheses on ecosystem processes and functional redundancy among communities.

Total species functional diversity—Huston (1994) characterized total species functional diversity as the number of different ecological functions performed by all species in a community times the mean number of species per function. Figure 34 presents estimates of total species functional diversity of vertebrates for terrestrial veg-

etation communities of the basin assessment area by using the ecological functions discussed above. Over all communities, the greatest vertebrate functional diversity is found in early seral montane forest, followed by upland woodlands and riparian woodlands, and upland shrublands. Historically, most vegetation cover types associated with early seral montane forest and upland woodlands have increased in total area in the inland West since early historic times, whereas those of riparian woodlands and upland shrublands have decreased. Vertebrate species within these cover types have shifted in relative abundance even if vertebrate functional diversity has remained more constant.

The lowest vertebrate functional diversity is found in early seral ponderosa pine forest, early seral subalpine forest, and agricultural lands (fig. 34). The vegetation cover types associated with early seral ponderosa pine forest communities have decreased in area since early historic

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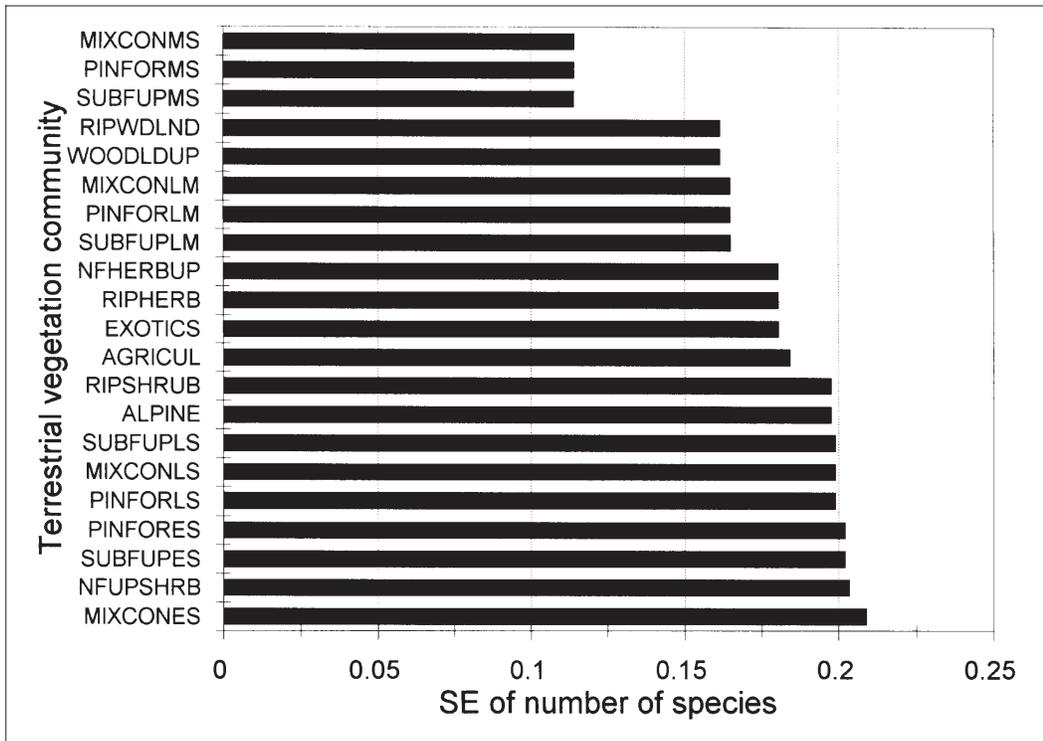
Figure 33—Variation in functional redundancy of KEFs among functions, displaying SE of number of species among KEF, by terrestrial vegetation community. Greater SE values denote greater variation in functional redundancy among KEFs (see table 2 for descriptions of terrestrial vegetation communities).

times; those associated with early seral subalpine forest communities have both increased and decreased; and agricultural lands have greatly increased. Interestingly, exotic vegetation communities do not rank particularly low in overall vertebrate functional diversity (fig. 34), although there are many vertebrate species that do not find suitable conditions in such habitats (Marcot and others 1997). Thus, levels of vertebrate functional diversity among vegetation comunities are complementary to—not coincident with—patterns of vertebrate species diversity (see Marcot and others 1997 for species diversity descriptions).

To what extent can we expect functional redundancy among vertebrate species with the same KEF? This question was addressed by Marcot and others (1997) who conclude that general functions, such as herbivory, cavity excavation, and pollination, might be considered redundant if performed by different species, but because each species has its unique combination of habitat associations and life history patterns, no two species can be expected to be exactly interchangeable. Thus, patterns of species functional diver-

sity presented here must be interpreted only as broad-scale geographic and macroecological trends and not interpreted as evidence for allowing any particular species loss or replacement in communities.

Climate Change and Species at Risk

Results of climate change modeling suggest potentially complex local and regional climate responses in the basin assessment area (see Hann and others 1997).[8] Potential changes in climate patterns among geographic locations within the basin assessment area are not consistent in indicating warming and drying trends, as suggested by Covington and others (1994) for the inland

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[8] Output from only one climate model—RegCM2, a regional climate model linked with a general circulation model to test regional responses to $2xCO_2$—is currently available for the basin assessment area. Hann and others (1997; also see footnote 2 in chapter 3) summarized results of that model along with knowledge of patterns that control regional climate.

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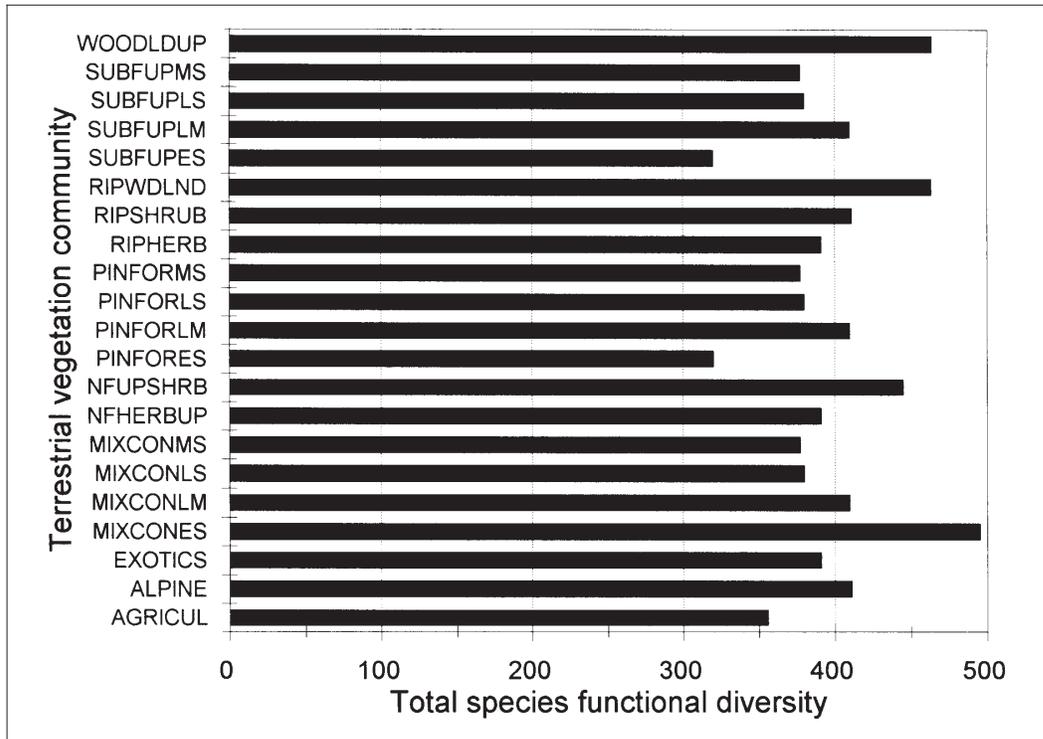
Figure 34—Total species functional diversity (number of KEFs per community times the mean number of species per function), by terrestrial vegetation community of the basin assessment area (see table 2 for description of terrestrial vegetation communities).

West,[9] and by general circulation models for boreal forests of high latitudes. The growing season could become +1 ^{o}C warmer with slightly greater spring precipitation (+5 percent) and slightly less autumn precipitation (-5 percent). Above 1000 m elevation, however, winter might experience slight cooling (-1 ^{o}C minimums and -2.5 ^{o}C maximums). This, along with significant increases in winter precipitation (+30 to 50 percent) could result in increased snow depth at high elevations, although the general circulation models reported by Covington and others (1994) suggest overall regional warming trends. Below 1000 m elevation, winter might experience significant warming (up to +3 ^{o}C minimums and maximums) (see footnote 2 in chapter 3).

Over all elevations, temporal changes in temperature and precipitation would not occur smoothly. Thus, individual plant species adversely affected would be those unable to adapt to changes or increases in interseasonal and interannual variation in temperature and precipitation. Mostly, climate changes and species-specific vegetation response in the basin assessment area are poorly known and not well modeled.

Given this uncertainty, we inspected the potential response of species to one possible aspect of climate change, namely, high-elevation warming during the growing season. Knoll (1984) noted that the effect of climatic change on extinctions of plant species depends less on absolute changes of mean annual temperature and precipitation, and more on successful migration of populations over generations to suitable areas. If suitable areas do not exist, such as caused by warming trends pushing upper elevation climate and life zones into more restricted distributions (that is, into areas of barren rock or ice, or even off the tops of mountains), or if access to suitable areas is blocked by dispersal barriers, then local extinction rates greatly increase. We do not know how these factors specifically will play out in the basin assessment area under climate-change scenarios, but we can surmise some general possible outcomes for upper elevation communities.

Upper elevation vegetation communities, particularly alpine tundra and subalpine forest communities, may experience higher summer temperatures and precipitation regimes. Under the "individual response" hypothesis (Gleason 1926, Grime 1977), plant species would respond individually and differently to climate changes (Covington and others 1994, Mehringer, n.d.). Mehringer (1995, n.d.) notes that upper elevation vegetation can respond rapidly to climate change; spruce (*Picea* spp.) and subalpine fir (*Abies lasiocarpa*) above treeline in the Canadian Rocky Mountains showed rapid upslope advances to >110 m above present treeline between 9,000 and 5,000 years ago and again near 1,000 years ago. Chapin and others (1995) note that arctic tundra has responded to climate changes by altered nutrient availability, growth-form composition, net primary production, and species richness.

Alpine tundra and subalpine forest communities currently are distributed among many mountain ranges with differing degrees of geographic isolation (fig. 35). At present in the basin assessment area, alpine tundra covers 95 100 ha (83 percent of this occurs on BLM or FS lands and 17 percent on other lands), and subalpine vegetation communities cover 6 633 600 ha (94 percent of this occurs on BLM or FS lands and 6 percent on other lands). Upward elevation shifts of these communities may result in increasing isolation of closely associated plant and animal species, reduction in overall distribution and area of occurrence in the basin assessment area, and local elim-

ination of these communities and closely associated species. Mehringer (n.d.) notes that, because of great topographic relief in the Columbia River watershed, even slight changes of temperature regimes and vegetation response can have a great influence on total areas of vegetation types.

Some of the hot spots of biodiversity and species rarity and endemism identified in Marcot and others (1997) occur on isolated mountain tops, and thus may be at risk from rapid climate changes. The degree of risk depends on how quickly the climate changes, how variable the climate becomes during the change period, and how well individual species can respond to such variability either through genetic plasticity or by changing aspect, elevation, or topographic location, as was found for Mojave species (Spaulding and others 1983). Topographic situation—such as mountain tops or upper elevation zones—may not be limiting if changes occur slowly enough to permit plant species to respond. One example of a hot spot of biodiversity in upper elevation or mountain settings is the eastern edge of the northern Cascade Range of Washington. In this area, glaciated landscapes, rounded peaks, high elevations, and subalpine climates provide for unique assemblages of amphibians and large carnivores, in contrast with the surrounding landscapes, and hold wetlands, bogs, and meadows that house many rare plants. Another biodiversity hot spot in mountain top settings is Glacier National Park and the higher elevations of Flathead National Forest in northwestern Montana, where rare large carnivores and intact rare plant communities occur in relatively undisturbed and isolated subalpine and alpine Rocky Mountain environments. Three examples of hot spots of species rarity and endemism in mountain top settings in Oregon include the crest of the Umatilla Mountains, where many west-side species are isolated and disjunct on these mountain tops; Wallowa Mountain peaks and Sacajewea peak, which hold disjunct Rocky Mountain and boreal species; and the Three Sisters area in Deschutes National Forest, which has unique volcanic substrates and geologic landforms that house locally endemic plants. Other examples are listed in Marcot and others (1997).

Other ecological aspects of upper elevation communities may be affected by shifts in precipita-

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[9] Covington and others (1994:45) report that "general circulation models (GCM) predict an increase of 1.5-2.5° C in mean annual temperature within the next 30 to 50 years.... Actual meteorological records for the 1980 decade and for the century indicate the Inland West region is particularly vulnerable to global warming and to extreme moisture stress." Results of the regional climate model simulations conducted for the present study, however, suggest a more complex picture for the basin assessment area (see footnote 2, chapter 3). The difference between the model predictions may be because of the difference in spatial resolution of the models. Covington and others do concur with transition conditions to a new, future equilibrium of (debatably) higher temperatures being marked by extreme climatic variability and discontinuities. Obviously, the final word on climate modeling and regional effects has not been written, and much work remains to be done, particularly in reconciling general circulation climate models with regional climate models.
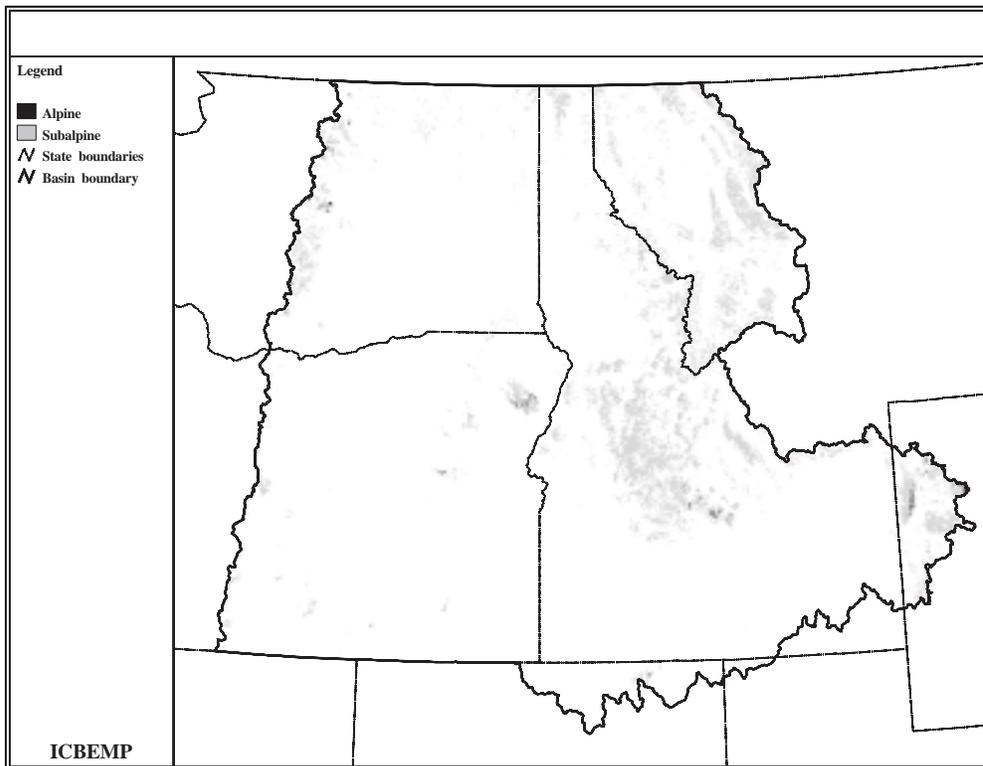
Figure 35—Current distribution of alpine tundra and subalpine forest communities in the basin assessment area.

tion, temperature, or disturbance (especially fire) regimes (Tausch and others 1993). As compared with lower elevation forests, subalpine forests are characterized by colder annual temperatures, heavy winter snowpacks, forest floors as important "sinks" of total ecosystem nitrogen ("loose" nitrogen cycles), greater importance of mycorrhizae in nutrient uptake, slower growth rates of trees, greater carbon allocation to root biomass, long retention of foliage, and long lifespan of trees (Vogt and others 1989), as well as high arboreal epiphyte loads and occurrence of some closely associated plant and animal species, including endemics. Some of these characteristics, particularly nitrogen sinks, retention of foliage, and lifespan of trees, may help buffer otherwise adverse community responses to quick changes in environmental conditions, including climate change. But other characteristics, particularly mycorrhizae importance, and occurrence of close associates and endemics, may impede quick "adaptation" to new climatic and disturbance regimes. Overall, potential changes in climate and disturbance patterns, and potential community response, are likely to be complex.

Local climate changes in lowland environments also may result in changes in fire regimes. Plants that respond differently to occurrence, intensity, frequency, and seasonality of fires likely would show differential increases or decreases under changing fire regimes. Marcot and others (1997) present a list of rare or potentially rare plants of the basin assessment area showing their orientation to fire regimes; this list can be consulted to hypothesize how species might respond. Results are quite mixed. For example, overstory lethal fires may benefit 7 lichen groups, 9 plant groups, and 9 vascular plant species, but harm a different set of 5 bryophyte groups, 11 lichen groups, 2 plant groups, and 11 vascular plant species. Increasing fire frequency, increasing fire-suppression activities, and changes in the seasonality of prescribed and natural fires—all of which may occur from regional changes in climate—also have mixed results.

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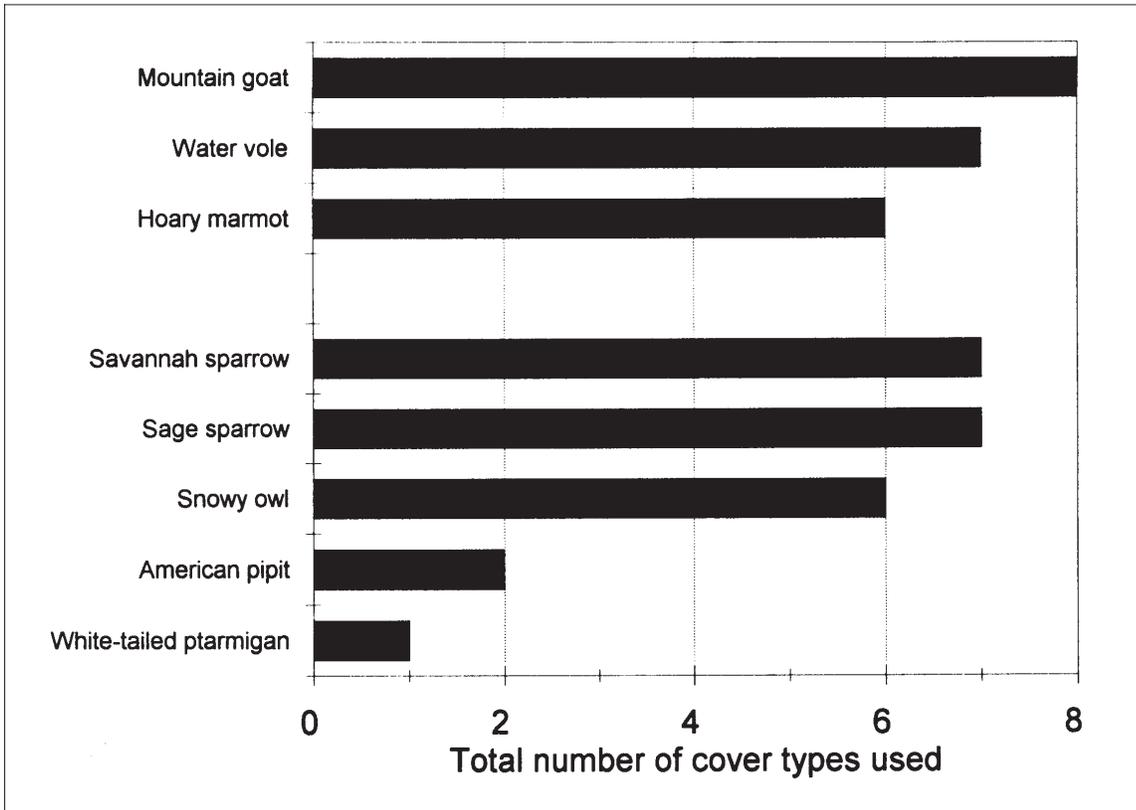
Figure 36—Vertebrate species at risk of regional warming trends, through decreases in total area of alpine tundra. Species shown are closely associated with alpine tundra vegetation communities (that is, occur in alpine tundra and <20 percent of all 44 vegetation cover types) in the basin assessment area.

Invertebrate responses to changes in fire regimes is poorly studied and largely unknown, except for forest insect pests (Hann and others 1997). Among vertebrates, stand-replacing fires can certainly change community composition. Hutto (1995) documented differential response by bird species to stand-replacement fires in the northern Rocky Mountains, and noted that one species— black-backed woodpecker (*Picoides arcticus*)— was nearly restricted to sites with standing fire-killed trees. Hutto also listed other bird species that may benefit over the long term from stand-replacement fires.

In some settings, vertebrate species may show clearer responses to changes in climatic conditions than would plants. We identified vertebrate species closely associated with upper elevation vegetation communities and thus possibly at greatest risk from upward altitudinal shifts of these life zones. In the basin assessment area, some 53 species—5 amphibians, 1 reptile, 22

birds, and 25 mammals—are associated with alpine tundra communities. Many of these species also occur in other vegetation communities. Eight of these species (5 birds and 3 mammals) are *closely* associated with alpine tundra communities (that is, occur in <20 percent of all 44 vegetation cover types) (fig. 36) and thus may be at greatest risk from warming trends. Of these eight species, white-tailed ptarmigan (*Lagopus leucurus*) is found solely in alpine tundra, and American pipit (*Anthus rubescens*) occurs in only one other vegetation cover type (that is, occurs in <10 percent of all 44 vegetation cover types). Ptarmigan and pipits are especially vulnerable to changes in alpine tundra communities.

Subalpine forest communities are potentially vulnerable to upper elevation warming trends (Graumlich 1991, Romme and Turner 1991, Schullery 1995), although Peterson (1995) reports that subalpine forests have been increasing in the West because of warmer climates. Peterson
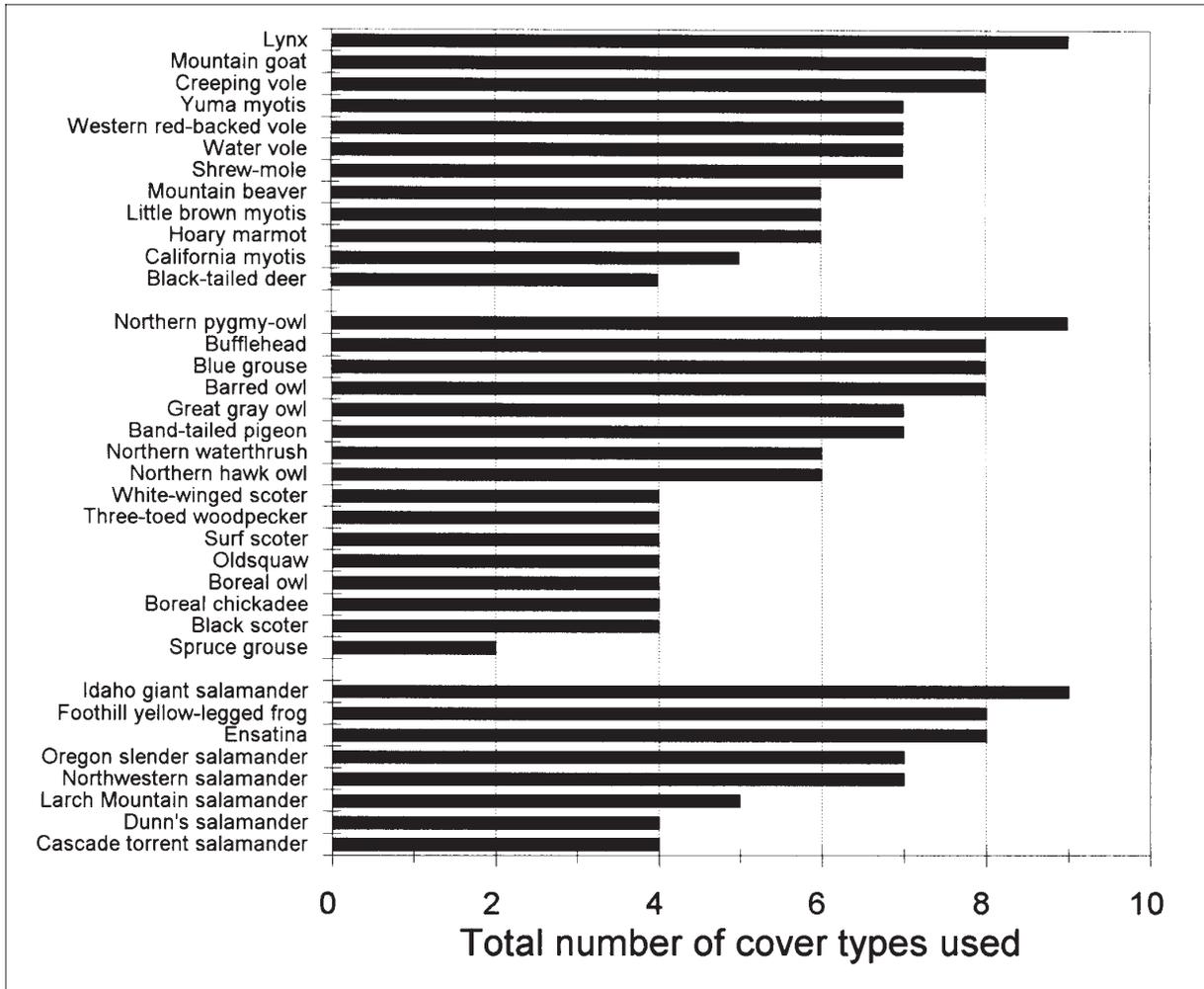
Figure 37—Vertebrate species at risk of regional warming trends, through decreases in total area of subalpine forests. Species shown are closely associated with subalpine forest vegetation communities (that is, occur in subalpine forests and <20 percent of all 44 vegetation cover types) in the basin assessment area.

(1995) also concludes that growth response of subalpine forests varies considerably according to geographic climate settings and microsite conditions. In the basin assessment area, subalpine forest communities include Engelmann spruce (*Picea engelmannii*)/subalpine fir forest, mountain hemlock forest, whitebark pine forest, and whitebark pine/subalpine larch forest cover types. Whitebark pine forest may be particularly vulnerable to climatic warming. Schullery (1995) projected that existing whitebark pine in Yellowstone National Park could decline by about 90 percent under a modest increase in warmth and dryness (also see Whitlock 1993).

A total of 205 vertebrate species—20 amphibians, 6 reptiles, 106 birds, and 73 mammals—are associated with subalpine forest communities. Of these, 36 species (8 amphibians, 16 birds, and 12 mammals) are *closely* associated with subalpine forest communities (that is, occur in <20 percent of all 44 vegetation cover types) and thus may be at particularly greater risk from upper elevation climatic warming (fig. 37). Of these 36 species, 13 occur in few other vegetation types (<10 percent of all 44 vegetation cover types) and are particularly vulnerable. Among these 13 highly vulnerable species, the salamanders include the regionally endemic Cascade torrent salamander

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and Dunn's salamander, and the locally endemic Larch Mountain salamander; the birds include spruce grouse (*Dendragapus canadensis*), boreal owl (*Aegolius funereus*), black scoter (*Melanitta nigra*), surf scoter (*M. perspicillata*), white-winged scoter (*M. fusca*), oldsquaw (*Clangula hyemalis*), three-toed woodpecker (*Picoides tridactylus*), and boreal chickadee (*Parus hudsonicus*); and the mammals include black-tailed deer (*Odocoileus hemionus columbianus*) and California myotis (*Myotis californicus*).

The three aforementioned regionally or locally endemic salamanders may be the most vulnerable of all 13 species in terms of changes of subalpine forest communities within the basin assessment area. The three aforementioned scoters occur in the basin assessment area as occasional migrants; the surf scoter is an occasional winter visitor, although the white-winged scoter has been recorded nesting in northeastern Washington. There is likely very little danger to the viability of any of the overall populations of scoters caused by habitat changes within the basin assessment area. Black-tailed deer ranges mostly west of the Cascade Range and occurs in the basin assessment area only along the high Cascade Range. Climate change might reduce the area of suitable habitat for black-tailed deer within the basin assessment area, although they likely would persist west of the crest of the Cascade Range. The rest of the subalpine forest community species listed above occur more regularly or more extensively within the basin assessment area.

We expect that increasing isolation of upper elevation environments might result in differential local isolation or extinctions of some animals, much as past rising temperatures likely drove some mammal species and their habitats upslope into disjunct distributions on mountaintop islands in the Great Basin (Diamond 1984). Likely survivors would include small mammals over big mammals of the same trophic status and habitat preference, habitat generalists over habitat specialists, and habitat generalist herbivores over similarly sized habitat generalist carnivores (Diamond 1984). In alpine tundra communities in the basin assessment area, such likely survivors might include the following herbivorous small mammals

(≤ squirrel size) that are habitat generalists (occur in ≥50 percent of all 44 vegetation cover types): deer mouse (*Peromyscus maniculatus*), Columbian ground squirrel (*Sperm ophilus columbianus*), golden-mantled ground squirrel (*S. lateralis*), long-tailed vole (*Microtus longicaudus*), and masked shrew (*Sorex cinereus*).

The converse of these criteria might describe mammal species more ecologically at risk of climate-induced changes in alpine tundra habitat. These species include big mammals (> squirrel size) over small mammals, habitat specialists (<50 percent of all 44 vegetation cover types) over habitat generalists, and habitat generalist carnivores over similarly sized habitat generalist herbivores. In the basin assessment area, the one at-risk mammal of alpine tundra fitting these criteria is wolverine.

Neilson (1991, 1993) and Noble (1993) note that ecotones between biomes may be sensitive areas to climatic change and therefore useful for monitoring change. Specifically, two types of change, boundary shifts of regions and physiognomic shifts within regions, are potentially independent because of differential species responses. Each type of change may require different strategies for monitoring.

The response of plant, invertebrate, and vertebrate communities to any directional changes in climate regimes likely will be made by individual species rather than by entire communities. In some cases, however, coadapted species complexes may suffer greater disruption than individual species' habitat associations may suggest. These complexes may include insect-plant pollination relations, invertebrate phoresis (especially dependence on other organisms for dispersal), mychorrhizal fungi-tree relations, and other mutualistic, commensal, and symbiotic relations.

For example, Clark's nutcracker (*Nucifraga columbiana*) is a key element in regeneration of whitebark pine—on the decline in the assessment area—by caching (burying) seeds in the ground. Clark's nutcracker occurs in 16 vegetation cover

types in the basin assessment area. It is unclear how complex shifts in plant species, vegetation cover types, and disturbance regimes resulting from climate change might affect Clark's nutcracker populations. Wells (1983) hypothesized that Clark's nutcracker (along with pinyon jay (*Gymnorhinus cyanocephalus*)) might have facilitated brisk redistribution of pinyon pine (*Pinus edulis*) in the intermountain West following rapid Holocene (Recent) climate changes. However, if local, high-elevation populations of Clark's nutcrackers become reduced and isolated because of warming-induced declines in total area of montane and subalpine forests (the species does not typically occur in alpine tundra communities or much below montane forest zones), there may be a compounding adverse affect on whitebark pine redistribution and viability (see Marcot and others 1997 for further discussions of other vertebrate species relations).

Another relation that might complicate species response to changing climatic and disturbance regimes is that of mycorrhizal fungi, their host tree species, and soils. Disturbances that reduce aeration or soil organic matter reduce mycorrhizal activity (Amaranthus and Perry 1994). Reduction in mycorrhizae reduces growth of many species of trees and retards productivity of soils. Some studies suggest that sites with harsh, continental climates (such as parts of the basin assessment area) may have lower fungal diversity than marine, coastal climates, and thus may be poorly buffered against changes in fungus populations caused by disturbance (Powers 1989) or by adverse climate change.

Climate change also has the potential to alter decomposition processes in grasslands and coniferous forests (Anderson 1991, Breymeyer and Melillo 1991, Esser 1992), plant respiration (Ryan 1991), phenology and growth of alpine vegetation (Walker and others 1994, 1995), bog formation (Foster and Wright 1990), and the role of soil in carbon sequestration (Van Veen and others 1991). Van Veen and others (1991) report that an increased level of CO_2 (a so-called "greenhouse gas") in the atmosphere likely will result in an increased input of organic carbon into the soil because of the expected increase in primary production. Whether this will lead to accumulation of greater amounts of organic carbon in soil depends on the flow of carbon through the plant into the soil, the tightness of the carbon cycle, and its subsequent transformation in the soil by microorganisms.

In this section, we have discussed potential future changes of terrestrial ecological communities and processes resulting from climate shifts. In the next section, we peer backwards and discuss prehistoric changes in climates and in the diversity of biota.

Paleoecology and Trends in Vertebrate Species and Communities of the Basin Assessment Area

Late Quaternary Conditions and Changes of the Basin Assessment Area

The Quaternary period (Pleistocene and Holocene [Recent] epochs of 1.64 million years ago to the present) represents a time of remarkably variable climates and biota in the inland West (McDonald 1984, Robbins 1993, Robbins and Wolf 1994). Climate cycles during this period were a major force in the evolution of plant response to change, so that, according to Tausch (1993), current plant communities today may be far less stable than they appear to be from our perspective.

Using pollen records from the late Quaternary, Mehringer (1985) reconstructed the following vegetation changes in selected sites of the inland West. Pollen sequences from the Holocene suggest fluctuations in vegetation resulting from short, acute climatic changes and from fire and volcanic episodes. Continental ice, alpine glaciers, and vast pluvial lakes had covered much of the area during the last glacial episode. Most of the northern Great Basin and adjacent provinces were covered by cold sagebrush-steppe conditions with montane conifers growing at lower elevations than they occur today.

Then, before 9,000 years ago during the early Holocene, a warming trend caused shrinking lakes, wasting glaciers, and catastrophic flooding (Allen and others 1986). Pioneer plants such as buffalo-berry (*Shepherdia canadensis* (L.) Nutt.) increased and forests spread northward, while

sagebrush-steppe spread southward as montane forests retreated to upper elevations. Douglas-fir began its spread to become a dominant element in conifer forests (Hermann 1985).

By 7,000 years ago, conifer forests lost ground to grasslands and sagebrush, and shadscale and sagebrush communities replaced grasslands. By 5,400 years ago, this trend slowed, and by 4,000 years ago, it reversed. A moister maritime climate developed in northern Idaho by 2,500 years ago or sooner, and fire regimes changed (Mehringer 1985). By the late Quaternary, lodgepole pine had spread north from Pleistocene glacial refuges farther south (Critchfield 1985). Relict lodgepole pine populations persisted in the Rocky Mountains (MacDonald and Cwynar 1985). Eventually, Douglas-fir became an important part of Northwestern forests during interglacial periods of the Quaternary (Hermann 1985).

The Quaternary fauna—known mostly from mammal records—was characterized by the spread of many large mammals throughout the inland West, as summarized by Potts and Behrensmeyer (1992). These included genera (1) now globally extinct, such as the mammoth (*Mammathus*), the bovid *Soergelia*, and saber-toothed cat (*Smilodon*); (2) extinct from the basin assessment area but persisting today elsewhere, such as jaguar (*Panthera*); and (3) persisting within the basin assessment area to this day, including wolf (*Canis*), mustelids (including ermine), moose (*Alces*), caribou (*Rangifer*), horse (*Equus*), cricetid rodents of genus *Clethrionomys*, hare (*Lepus*), and vole (*Microtus*). Five Quaternary families of artiodactyls occurred, including bovids, camelids, and antilocaprids, as well as xenarthrans, including glyptodonts, armadillos, and ground sloths. Proboscideans included gomphotheres and mastodonts in addition to the mammoths. Cricetid rodents underwent exceptional adaptive radiation during the Plio-Pleistocene as savanna and grassland ceded to steppe environments.

During the Pleistocene, rodents diversified, while other groups (proboscideans, perissodactyls, xenarthrans, and camelids) reduced. Immigrants across the Bering land bridge to the area during this time included bison (*Bison*), mountain sheep (*Ovis*), muskox (*Ovibos*), moose (*Alces*), lion (*Panthera*), and humans (*Homo sapiens*) (Pileou 1991). Climatic fluctuations served to blend biotas during this time, mixing these newcomer immigrants with the existing resident saber-toothed cat, dire wolf (*Canis*), horse, mammoth, many squirrels (sciurids), New World rodents (cricetids), and bovids (Potts and Behrensmeyer 1992).

In the late Pleistocene, large mammals suffered waves of extinctions between 15,000 and 9,000 years ago. This "megafaunal extinction" took out mammoths, mastodonts, gomphotheres, saber-toothed cats, dire wolves, horses, sloths, camels, and many species of bears, deer, antilocaprids, and others. It may be important to understand the reasons for these extinctions—as yet, they are not fully understood—to better interpret potential effects of our modern day changes in climates and habitats. Causes of the megafaunal extinction episodes have been variously attributed to human hunting, climate changes and associated habitat shifts during the early interglacial periods, interspecific competition, and differential resorting of species into increasingly disjunct communities (Martin and Klein 1984).

Glacial cycles in the Holocene caused many mammalian taxa to separate in distribution as habitats became more patchy and disjunct and as mammal species responded individually to changing environments (Potts and Behrensmeyer 1992). The resulting communities have been called nonanalogue communities or disharmonious faunas. Such faunas had high beta diversity of species among geographic locations, such as different mountain ranges. Some authors attributed these changes and the persistence of non-analogue communities to periods of more equable climates (Potts and Behrensmeyer 1992).

Several important lessons for interpreting present-day biota in the basin assessment area can be learned from this brief review of Quaternary period changes over the span of a dozen millennia:

1. Climate shifts have occurred unpredictably and have signalled great changes in both distribution and species composition of floras and faunas.

2. Episodic extinctions of at least large mammals have occurred, perhaps associated with climate change, human hunting pressure, or other factors.

3. Differential extinctions and originations (speciation and immigration of existing species) have occurred mostly with unpredictable patterns but over periods of millennia. Examples are the great reduction in artiodactyls (especially horses) and the increase in diversity of cricetids (mice and rats) and sciurids (squirrels and chipmunks).

4. Separation and isolation of species because of climatic shifts resulted from differential response and sorting by species during periods of climate change and equilibration.

At least as a working hypothesis, we might conjecture that today's biotas of the basin assessment area might respond with such similar, general patterns to increasing environmental pressures, changing habitats, and potentially shifting climates. Unknowns in this hypothesis include (a) rates of response of species, assemblages, and ecological communities, which may be unable to adequately respond and thereby might vanish; (b) species-specific changes that may ensue, although we can now draw from databases on species-environment relations to begin to frame specific predictions (for example, see the section above on potential near-future climate change); and (c) how effects of human activities might compound with background natural variations in climates and environments in affecting species and ecological communities. In this vein, historic and current human activities of greatest concern on Federal lands include short-term changes of natural disturbance regimes such as fire, and human activities directly affecting populations or habitats including hunting, urbanization, livestock grazing, mining, and timber harvesting.

Two still-unanswered questions about climate change during the Quaternary within the basin assessment area may prove of interest to management:

1. An explicit test is needed of the null hypothesis that the range of historic conditions (past 50 to 200 years) does not reflect the range of prehistoric (Holocene) conditions, in terms of climate and vegetation. To test this hypothesis, one might use pollen diagrams of vegetation change (for example, Mehringer 1985) as compared with the

projections of historic vegetation conditions (Hann and others 1997).

2. An explicit test is needed of the null hypothesis that there is no long-term (Holocene or Quaternary) set of repeating conditions of climate and vegetation patterns within which an idealized, stable range of natural variability (sensu Morgan and others 1994) can be estimated. This hypothesis can be tested by calculating a running SE of climate parameters or vegetation conditions (as taken from pollen profiles), as a function of time, and determining if it reaches an asymptote, thus signifying a stable range of natural variability.

The first question above is important in determining if the range of historic conditions truly provides for environmental conditions in which species immigrated or evolved, and in which communities developed. The second question is important for testing the very concept of range of natural variability.

Assuming that understanding the past and present helps us project the future, additional work on the following ecological topics would prove useful:

1. Identify Quaternary source pools of species, zones and directions of spread of species, and species dispersal dynamics, rates, and barriers.

2. Identify evolutionary adaptations and selection mechanisms during the Quaternary, including allopatric speciation, character divergence among sympatric species, isolating mechanisms, and species swamping.

3. Study reproductive ecology pertinent to understanding adaptations, including hybridization (Samson and Knopf 1994).

4. Study development of keystone roles of species and their expression in changing environments and communities.

5. Identify changes in endemism by taxonomic level and proportion of taxa, and mechanisms causing endemism (such as Pleistocene refugia, allopatric or sympatric speciation, and isolation by physiographic conditions such as montane islands, flood-carved gorges, and scabland landscapes).

Tertiary Biota and Comparison With Extant Vertebrates in Eastern Oregon

Work at John Day Fossil Beds National Monument has described the ancient (pre-Pliocene epoch, Tertiary period) flora and fauna of eastern Oregon (Retallack and others 1996).[10] The beds occur in several arms of the John Day River system in what is now mainly grazed rangeland, agriculture land, and some sagebrush-steppe habitat. Fossil records from the beds span more than 40 million years and date from 45 to 5 million years ago. Although a few amphibians, reptiles, and one raptor have been identified in fossil records at the beds, the most diverse fossil evidence is that of medium- to large-sized mammals. At the beds, some 12 orders, 47 families, 155 genera, and 298 species of mammals have been identified spanning the 40-million-year period (fig. 38; see footnote 10).

Of these Tertiary taxa, 8 orders (67 percent), 16 families (34 percent), 5 genera (3 percent), and no species (0 percent) remain extant in the basin assessment area (fig. 39). The Tertiary mammal genera still exant from the Tertiary are two carnivora, *Martes* (Mustelidae) and *Canis (Canidae);* two rodentia, *"Sciurus"* and *Spermophilus* (both Sciuridae); and a chiropteran bat, *Myotis* (Vespertilionidae). In addition, still extant in the basin assessment area are the amphibian (frog) *Rana* (Ranidae), and the turtle *Clemmys* (Testudinidae). The current species found within the general basin assessment area representing these ancient forms are listed in table 9. These are taxa of particular paleoecological interest because of the antiquity of the genera. Fossils of all these ancient genera were taken from formations representing the mid-late Miocene (8 to 6 million years ago), the most recent of the Tertiary formations in John Day Fossil Beds. An exception was "*Sciurus*," which came from the much older formations spanning the late Eocene, Oligocene, and early Miocene (39 to 20 million years ago). In addition, *Clemmys* and *Martes* also were found in formations from the mid-Miocene (15 to 12 million years ago).

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[10] Personal communication. 1996. T. Fremd, John Day Fossil Beds National Monument, John Day, Oregon.

Many other ancient families are still extant in the basin assessment area even though none of their Tertiary genera has survived. These ancient families, listed in table 10, include those given above as well as additional families of turtles, lizards, avian raptors, marsupials, carnivores, horses, pronghorns, rodents, and rabbits.

In comparison, the total extant mammal fauna of the basin assessment area consists of 8 orders, 24 families, 67 genera, and 132 species (fig. 38). Compared to all mammalian fossil taxa discovered at John Day Fossil Beds, the number of extant orders is 67 percent of the total number of Tertiary orders; families are 51 percent; genera are 43 percent, and species are 44 percent. In terms of taxonomic richness (number of taxa), then, the Tertiary mammal fauna was far richer than that at present, at all taxonomic levels.

This comparison, however, is uneven in several ways. (1) The fossil record differentially preserves evidence of species with various life forms, body size, and habitat associations. For example, bats are represented by only a single species in the fossil records of the beds, whereas the current bat fauna includes some 15 species; more than a single species probably existed prehistorically, but other species have not been preserved or detected yet in the fossil record. As well, rare species probably often go undetected in fossil records (Koch 1978). (2) The mammalian fossil records at the beds represent an enormous span of time as compared with today's "snapshot," which is taken over a much broader geography of the basin assessment area. Results of the above comparisons would be even more exaggerated if confined to just the extant sagebrush-steppe fauna, because the current local biota of just the sagebrush-steppe environment of eastern Oregon is substantially less diverse than that of the full basin assessment area. (3) Taxonomic problems of comparison include the fact that species are more difficult toidentify in the fossil record than are orders or families, and prehistoric morphospecies do not exactly coincide with current species in terms of equivalent systematics. Still, the differences between prehistoric and extant number of taxa
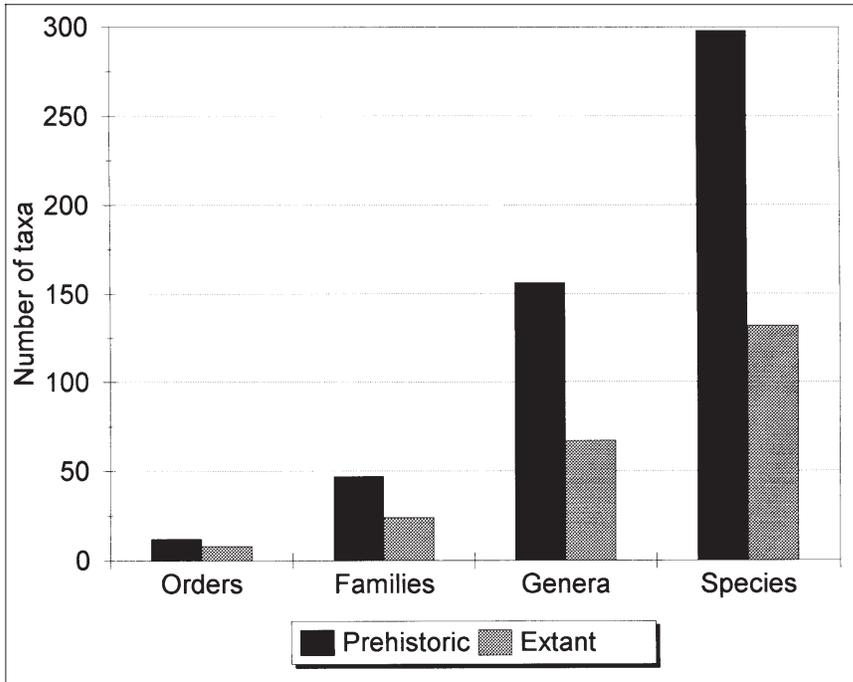
Figure 38—Biodiversity (number of taxa) of prehistoric (Tertiary) mammals of John Day Fossil Beds, eastern Oregon; and extant (still living) mammals of the basin assessment area. (Source of Tertiary biodiversity information: see footnote 10 in chapter 4.)
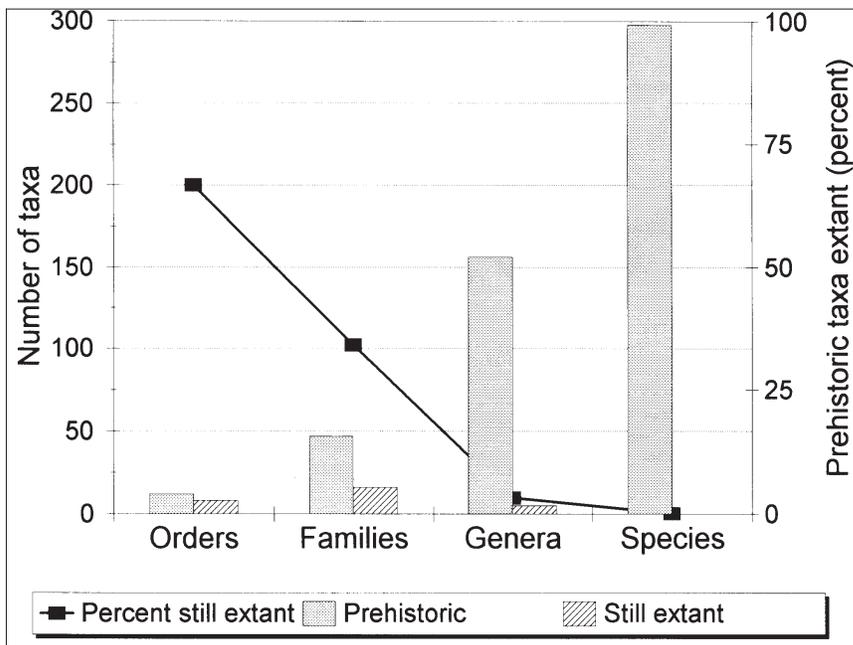

Figure 39—Biodiversity of prehistoric (Tertiary) mammals of John Day Fossil Beds, eastern Oregon, showing number and percentage of prehistoric taxa persisting to the present.

Table 9—Currently extant species or subspecies of vertebrates occurring in the basin assessment area that are represented by Tertiary genera discovered in John Day Fossil Beds National Monument, eastern Oregon, including the formation in which each genus was discovered[a b]

Tertiary genus	Extant species or subspecies	Order, family	Formation[c]
Rana	*R. aurora*, red-legged frog	Anura, Ranidae	A
	R. boylii, foothills yellow-legged frog		
	R. cascadae, Cascades frog		
	R. catesbeiana, bullfrog		
	R. clamitans, green frog		
	R. luteiventris, spotted frog		
	R. pipiens, northern leopard frog		
	R. sylvatica, wood frog		
Clemmys	*C. marmorata*, western pond turtle	Chelonia, Testudinidae	A, B
Martes	*M. americana*, American marten	Carnivora, Mustelidae	A, B
	M. pennanti, fisher		
Canis	*C. latrans*, coyote	Carnivora, Canidae	
	C. lupus, gray wolf		A
"*Sciurus*"	*S. griseus*, western gray squirrel	Rodentia, Sciuridae	C
	S. niger, eastern fox squirrel		
Spermophilus	*S. armatus*, Uinta ground squirrel	Rodentia, Sciuridae	A
	S. beecheyi, California ground squirrel		
	S. beldingi, Belding's ground squirrel		
	S. brunneus, Idaho ground squirrel		
	S. columbianus, Columbian ground squirrel		
	S. elegans nevadensis, Wyoming ground squirrel		
	S. lateralis, golden-mantled ground squirrel		
	S. saturatus, Cascade golden-mantled ground squirrel		
	S. townsendii, Townsend's ground squirrel		
	S. washingtoni, Washington ground squirrel		
Myotis	*M. californicus*, California myotis	Chiroptera, Vespertilionidae	A
	M. ciliolabrum, western small-footed myotis		
	M. evotis, long-eared myotis		
	M. lucifugus, little brown myotis		
	M. thysanodes, fringed myotis		
	M. volans, long-legged myotis		
	M. yumanensis, Yuma myotis		

[a] See footnote 10 in chapter 4.

[b] These living taxa belong to ancient genera and are of particular evolutionary and biogeographical interest. All species and subspecies listed here are currently found within the basin assessment area although not necessarily at John Day Fossil Beds.

[c] Formations: A = mid to late Miocene, 8 to 6 million years ago; B = mid to Miocene, 15 to 12 million years ago; and C = late Eocene, Oligocene, and early Miocene, 39 to 20 million years ago.

Table 10—Currently extant taxa of vertebrates occurring in the basin assessment area that are represented by Tertiary families discovered in John Day Fossil Beds National Monument, eastern Oregon, including the formation in which the family was discovered[a] [b]

Tertiary family still extant	Extant representative genera	Order	Formation[c]
Ranidae	*Rana*—true frogs	Anura	A
Chelydridae (=Emydidae, part)	*Chrysemys*—turtles	Chelonia	D
Testudinidae (=Emydidae, part)	*Clemmys*—turtles	Chelonia	A, B
Boidae	*Charina*—boas	Squamata	C
Falconidae	*Falco*—falcons	Falconiformes	B
Didelphidae	*Didelphis*—opossum	Marsupalia	C
Mustelidae	*Gulo*—wolverine		
	Lutra—otter		
	Martes—marten, fisher		
	Mephitis—skunk		
	Mustela—ermine, weasels		
	Spilogale—skunk		
	Taxidea—badger		
Procyonidae	*Procyon*— raccoon	Carnivora	B
Canidae	*Canis*—coyote, wolf	Carnivora	A, B, C
	Urocyon—gray fox		
	Vulpes—kit fox, red fox		
Ursidae	*Ursus*—bears	Carnivora	A, C
Equidae	*Equus*—horse	Perissodactyla	A, B, C, D
Antilocapridae	*Antilocapra*—pronghorn	Artiodactyla	A, B
Aplodontidae	*Aplodontia*—mountain beaver	Rodentia	C
Castoridae	*Castor*—beaver	Rodentia	A, B, C
Cricetidae (=Muridae, part)	*Clethrionomys*—red-backed voles	Rodentia	A, C
	Lemmiscus—vole		
	Microtus—voles		
	Mus—mouse		
	Neotoma—woodrats		
	Ondatra—muskrat		
	Onychomys—grasshopper mouse		
	Peromyscus—mice		
	Phenacomys—vole		
	Rattus—rats		
	Reithrodontomys—harvest mouse		
	Synaptomys—lemming		

Table 10—Currently extant taxa of vertebrates occurring in the basin assessment area that are represented by Tertiary families discovered in John Day Fossil Beds National Monument, eastern Oregon, including the formation in which the family was discovered[a][b] (continued)

Tertiary family still extant	Extant representative genera	Order	Formation[c]
Geomyidae	*Thomomys*—pocket gophers	Rodentia	B, C
Heteromyidae	*Dipodomys*—kangaroo rats	Rodentia	B, C
	Microdipodops—kangaroo rat		
	Perognatus—pocket mice		
Sciuridae	*Ammospermophilus*—antelope squirrel	Rodentia	A, B, C
	Glaucomys—flying squirrel		
	Marmota—marmots		
	Sciurus—squirrels		
	Spermophilus—ground squirrels		
	Tamias—chipmunks		
	Tamiasciurus—forest squirrels		
Leporidae	*Brachylagus*—pygmy rabbit	Lagomorpha	A, B, C
	Lepus—hare, jackrabbits		
	Sylvilagus—cottontails		
Vespertilionidae	*Antrozous*—bat	Chiroptera	A
	Eptesicus—brown bat		
	Euderma—bat		
	Lasionycteris—bat		
	Lasiurus—bat		
	Myotis—myotis (bats)		
	Pipistrellus—pipistrelle (bat)		
	Plecotus—big-eared bat		

[a] See footnote 10 in chapter 4.

[b] These ancient families are of particular evolutionary and biogeographical interest. Extant representative genera of these ancient families are listed; most of these genera are not present in the Tertiary fossil record (see table 9).

[c] Formations: A = mid to late Miocene, 8 to 6 million years ago; B = mid Miocene, 15 to 12 million years ago; C = late Eocene, Oligocene, and early Miocene, 39 to 20 million years ago; and D = early to mid Eocene, 54 to 37 million years ago.

(fig. 39) suggest that the "turnover" rate (extirpation or extinction, as compared with formation or invasion of new taxa in the area) has been increasing, from least to most, in orders, families, genera, and species.

At the beds, mammalian diversity of taxa within orders can be depicted. In the fossil record of the Tertiary, several orders were particularly rich in numbers of families, genera, and species. Listed in sequence of decreasing number of component taxa, they were Artiodactyla, Carnivora, Rodentia, and Perissodactyla (fig. 40). Among extant forms, the more diverse orders (in decreasing sequence) are Rodentia, Carnivora, Chiroptera, Artiodactyla, and Insectivora (fig. 41). This comparison suggests major declines in diversity of perissodactyls. Webb (1984) outlined declines in horses of North America, which area major portion of the fossil record of perissodactyls of John Day Fossil Beds; and Gingerich (1984) noted that some 56 percent of Wisconsinan perissodactyls disappeared from the North American fauna without taxonomic replacement (although the general ecological function of herbivory has been continued with the appearance of new cricetid and sciurid species). Artiodactyls, carnivores, and rodents have always been diverse, although consisting of different families, genera, and species over geologic time. Insectivores and
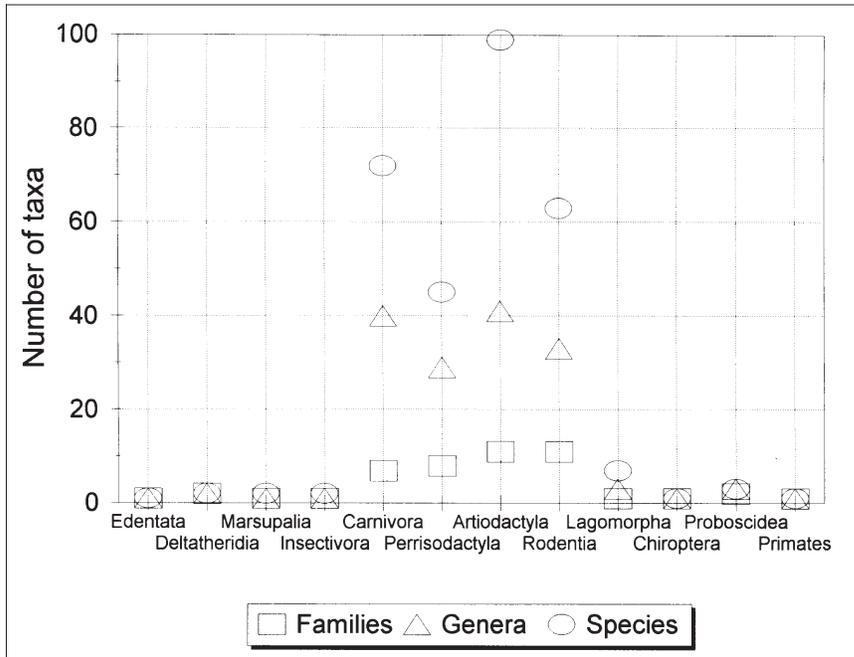
Figure 40—Diversity of families, genera, and species among orders of prehistoric (Tertiary) mammals of John Day Fossil Beds, eastern Oregon (see text for sources).
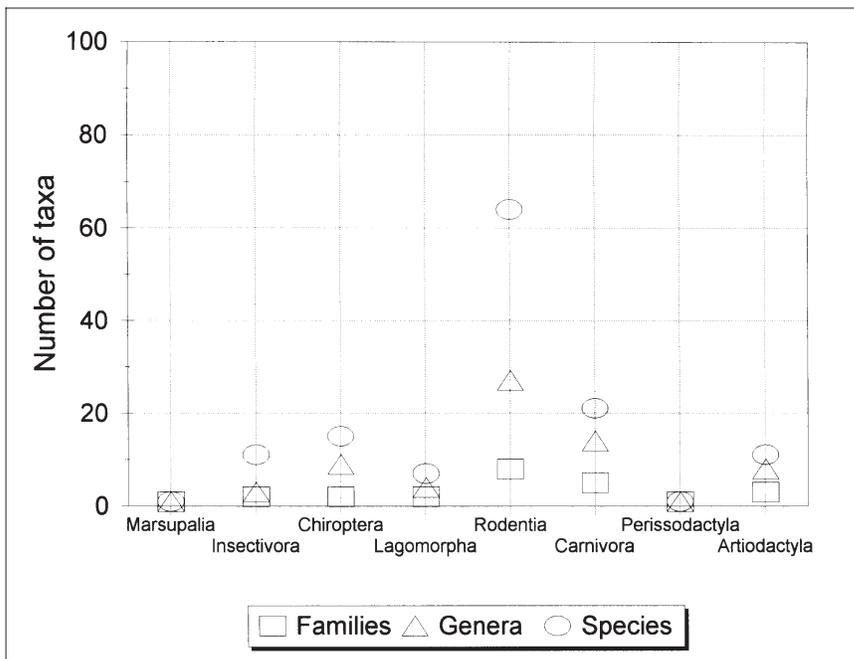

Figure 41—Diversity of families, genera, and species among orders of extant mammals of the basin assessment area. Note that the vertical axis is scaled the same as in figure 40.

chiropterans may have increased in diversity or may simply be underrepresented in the fossil record. Overall diversity of mammalian families, genera, and species among orders, calculated by using the Shannon-Weiner diversity index, are nearly identical in comparing Tertiary to current faunas (fig. 42). Thus, overall mammalian diversity has remained more or less constant, although taxonomic composition of the fauna—especially below order level—has turned over.

Records from different formations of John Day Fossil Beds also have allowed reconstruction of several major climatic periods (Chaney 1956, Retallack and others 1996; see footnote 10):

1. Fifty-four to 37 million years ago (Clarno Formation; early to mid Eocene epoch)—Tropical to subtropical forests covered the area. Plants included hundreds of species, many new to science, now preserved in fossils of seeds, nuts, fruits, leaves, branches, stems, and roots. Mammals included browsing bonototheres and amynodonts, hyaenadonts, and *Patriofelis* predators.

2. Thirty-nine to 20 million years ago (John Day Formation; late Eocene, Oligocene, early Miocene epochs)—Environments were diverse in the John Day Fossil Beds region, with deciduous forests replacing the earlier subtropical forests. Early Miocene flora was highly diverse. The fauna included many mid- to large-sized mammals, such as dogs, cats, swine, oreodonts, horses, camels, rhinoceroses, and rodents. Volcanic eruptions then occurred between 20 and 15 million years ago.

3. Fifteen to 12 million years ago (Mascall Formation; mid Miocene epoch)—Highly fertile soils of the region, along with a moderate climate, led to development of grassland and mixed-

hardwood woodlands during this period. The fauna included horses, camels, deer, bears, weasels, dogs, and cats. Large mammals included gomphotheres, rhinos, and bear-dogs.

4. Eight to 6 million years ago (Rattlesnake Formation; mid to late Miocene epoch)—During this period, the climate may have become dryer and cooler, and the environment dominated by grasslands. Evidence of horses, sloths, rhinos, camels, peccaries, pronghorns, dogs, bears, and other species has been found.

This record by formation at John Day Fossil Beds provides an opportunity to compare prehistoric to current vertebrate faunas by general time period (fig. 43). Numbers of taxa among families, genera, and species become increasingly disparate across these formations and periods. The period of 39 to 20 million years ago (John Day Formation) seems to harbor the greatest diversity in known fossils of families and genera. Current diversity of families and genera of the basin assessment area does not match that of this time period, and would even be far less if only current-day mid- and large-bodied mammals (to match those taxa more likely to persist and be discovered in the fossil record) of sagebrush-steppe communities were considered.

Ecological Integrity of Terrestrial Species and Communities

In this section, we depict current ecological integrity of the basin assessment area for terrestrial ecosystems. Karr (1990) urged that protection of biodiversity be one aspect of protecting the biological integrity of natural resource systems. Several studies (for example, Karr 1991, Kerans and Karr 1994) have used a broadly based, multi-parameter index of biotic integrity (IBI) for measuring environmental quality of aquatic ecosystems and status of fish assemblages. Other aspects
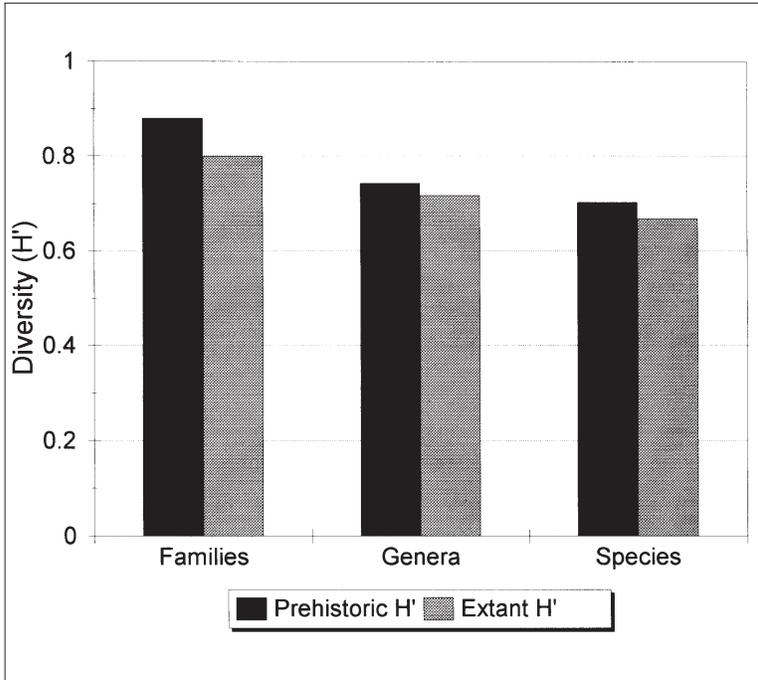
Figure 42—Shannon-Weiner diversity of families, genera, and species among orders of prehistoric (Tertiary) and extant mammals of John Day Fossil Beds and the basin assessment area, respectively.
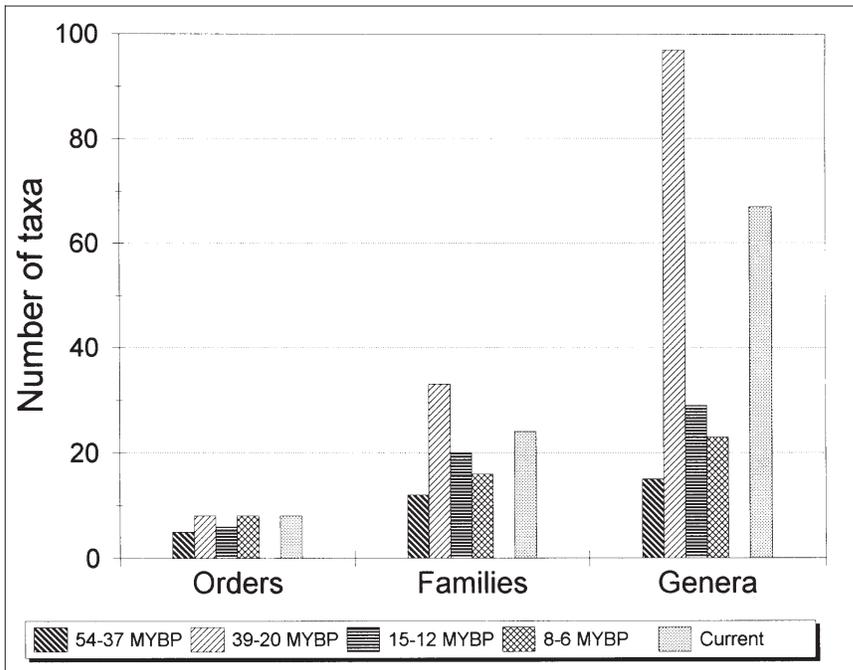

Figure 43—Number of orders, families, and genera of mammals by formation (Tertiary period, John Day Fossil Beds, eastern Oregon) and at present (basin assessment area). MYBP = million years before present.

of measuring ecological integrity, however, also could pertain to long-term viability and evolutionary potential of species, and long-term environmental conditions. We expand on the IBI approach by including these additional components in our evaluation of ecological integrity of terrestrial species and communities of the basin assessment area.

Haynes and others (1996) assumed six possible goals that may be of use for managing ecological integrity of Federal lands in the basin assessment area. Three of the six goals pertain to terrestrial ecological conditions. They are consistent with, but were not necessarily modeled after, goals for maintaining ecological integrity as listed by Grumbine (1994). We assumed that the three goals may provide useful benchmarks for measuring progress for at least some of the terrestrial components of ecological integrity. The three goals are to maintain species viability, maintain long-term evolutionary potential of species, and manage for multiple ecological domains and evolutionary timeframes.

In this analysis, we divided each of these three goals into subcomponents. For each component, we identified specific GIS themes representing current conditions, as follows:

Ecological integrity goal 1—Maintain species viability

Species components:

- Component (1a)—Distribution of threatened and endangered vertebrate species
- Component (1b)—Distribution of threatened and endangered plants
- Component (1c)—Distribution of locally endemic vertebrate species
- Component (1e)—Distribution of rare plants (as listed in Natural Heritage databases)

- Component (1f)—Distribution of candidate category C1 and C2 vertebrate species as listed by USDI Fish and Wildlife Service[11]

Habitat connectivity component:

- Component (1d)—Distribution of vertebrate species occurring along key habitat corridors

Ecological integrity goal 2—Maintain long-term evolutionary potential of species

Species component:

- Component (2a)—Distribution of disjunct vertebrate species populations

Diversity components:

- Component (2b)—Mapped locations of biodiversity hot spots (plants and vertebrates combined)
- Component (2c)—Mapped locations of species rarity and endemism hot spots (plants and vertebrates combined)
- Component (2d)—Mapped locations of centers of concentration of biodiversity, and of species rarity and endemism (plants and vertebrates combined)

_____

[11] This chapter reports on analyses conducted through October 1995. Since that time, USDI Fish and Wildlife Service has published a change in their species status program, essentially replacing the three candidate species categories with a single category of candidates for listing with a 1-year review period of this program change (Federal Register, February 28, 1996, vol. 61, no. 40, p. 7596). In this change, most of the species that were classified as category 2 or 3, and 303 taxa that were category 1 candidates, are no longer included in the list of candidate species. Many plant and animal species addressed in this assessment were denoted as candidate category 1 or 2 when the data were gathered. Of those 131 category 1 or 2 plants, 4 became candidates in the Federal Register notice: *Castilleja christii, Erigeron basalticus, Sidalcea oregana* var. *calva,* and *Thelypodium howellii* spp. *spectabilis*. Of those 34 category 2 animals (none had been designated category 1 in the basin assessment area), only mountain plover (*Charadrius montanus*) and spotted frog (*Rana luteiventris*, prev. *R. pretiosa*) were still designated as candidates. All other plants and animals were dropped from the list of candidates. This assessment chapter, however, retains the listings for two reasons: (1) our analyses and data collection preceded the ruling change; and (2) our charge was to address species' ecologies and conservation status, and the category 2 status in particular still helps to denote species of potential conservation concern deserving attention in this charge.

Ecological integrity goal 3—Manage for multiple ecological domains and evolutionary timeframes

Peripheral species and unique vertebrate assemblages by ERU:

- Component (3a)—Upper Klamath Basin species

- Component (3b)—Owyhee Upland species

- Component (3c)—Northern Great Basin species

- Component (3d)—Amphibians of the Columbia Gorge

- Component (3e)—Snake River Headwaters ERU and western Wyoming species

- Component (3f)—Upper Snake River ERU species

    Component (3g)—Western Montana species

Full trophic ladder component:

- Component (3h)—Vertebrate carnivores

For each component, we produced a Paradox® database and an ArcInfo® GIS map theme to show locations or distributions of conditions by 4th code HUC. Specific results are as follows, along with further discussions of the ecological foundation for each goal and its components.

Ecological Integrity Goal 1: Maintain Species Viability

One aspect of ecological integrity pertains to the viability of species. Several authors have developed various assessments of species components for various ecosystems. Lyons and others (1995) list 10 components of fish assemblages in west-central Mexico that they judged representative of ecological conditions of species and their habitats. The components they used included number of native species, number of sensitive species, and percentage of exotic species. Karr (1991) and Kerans and Karr (1994) assessed water quality integrity by measuring attributes of fish assemblages. In similar fashion, we identified a series of mappable species and diversity components for this first goal.

Species components—The following five integrity components relate to distribution of sets of species of particular concern for maintaining species viability.

Component (1a): Distribution of threatened and endangered vertebrate species—Eight federally listed threatened or endangered vertebrates occur in the basin assessment area. Geographic information systems maps of species range distributions were available for seven (table 11). Distribution of marbled murrelet (*Brachyramphus marmoratus*) was not mapped; habitat for this species occurs at the extreme periphery of its range within the basin assessment area in the Cascade Range in northern Washington. The database and map constructed for this component display the number of threatened and endangered vertebrate species by 4th code HUC (fig. 44). More threatened and endangered vertebrate species are located in the Cascade Range in northern Washington, the northern glaciated mountains of northern Idaho and western Montana, central Idaho mountains, and the Greater Yellowstone Ecosystem than elsewhere throughout the basin assessment area.

Component (1b): Distribution of threatened and endangered plants—Four federally listed threatened or endangered plants occur within the basin assessment area (table 12). Range locations (point locations of site occurrences) were taken from state Natural Heritage Program databases. The database and map constructed for this component display number of threatened and endangered plant species by 4th code HUC (fig. 45). Threatened and endangered plants occur scattered singly in six general locations in the basin assessment area: the Washington-Idaho border, the Hell's Canyon area of Oregon and Idaho, western Montana, southern Idaho, south-central Oregon, and the Klamath Basin portion of Oregon.

Component (1c): Distribution of locally endemic vertebrates—Some seven vertebrate taxa (species or subspecies) are locally endemic within the basin assessment area (table 13). The database and map for these species display percentage of the area of each 4th code HUC with coverage by any or all of these species (fig. 46). Most locally endemic vertebrates occur in eastern Washington, central Idaho mountains, and most of the southern tier of the basin assessment area through southern Oregon, southern Idaho, and adjacent states.

Component (1e): Distribution of rare plants (as listed in Natural Heritage databases from the

Table 11—Threatened (T) or endangered (E) vertebrates of the basin assessment area

Species code	Scientific name	Common name	Status
FALPER	*Falco peregrinus*	Peregrine falcon	E
GRUAME	*Grus americana*	Whooping crane	E
HALLEU	*Haliaeetus leucocephalus*	Bald eagle	T
STROCA	*Strix occidentalis caurina*	Northern spotted owl	T
BRAMAR	*Brachyramphus marmoratus*	Marbled murrelet	T
RANTCA	*Rangifer tarandus caribou*	Woodland caribou	E
URSARC	*Ursus arctos*	Grizzly bear	T
CANLIR	*Canis lupus*	Gray wolf	E

Legend
- Species = 1
- Species = 2
- Species = 3
- Species = 4
- 4th field hydrologic units
- State boundaries
- Basin boundary

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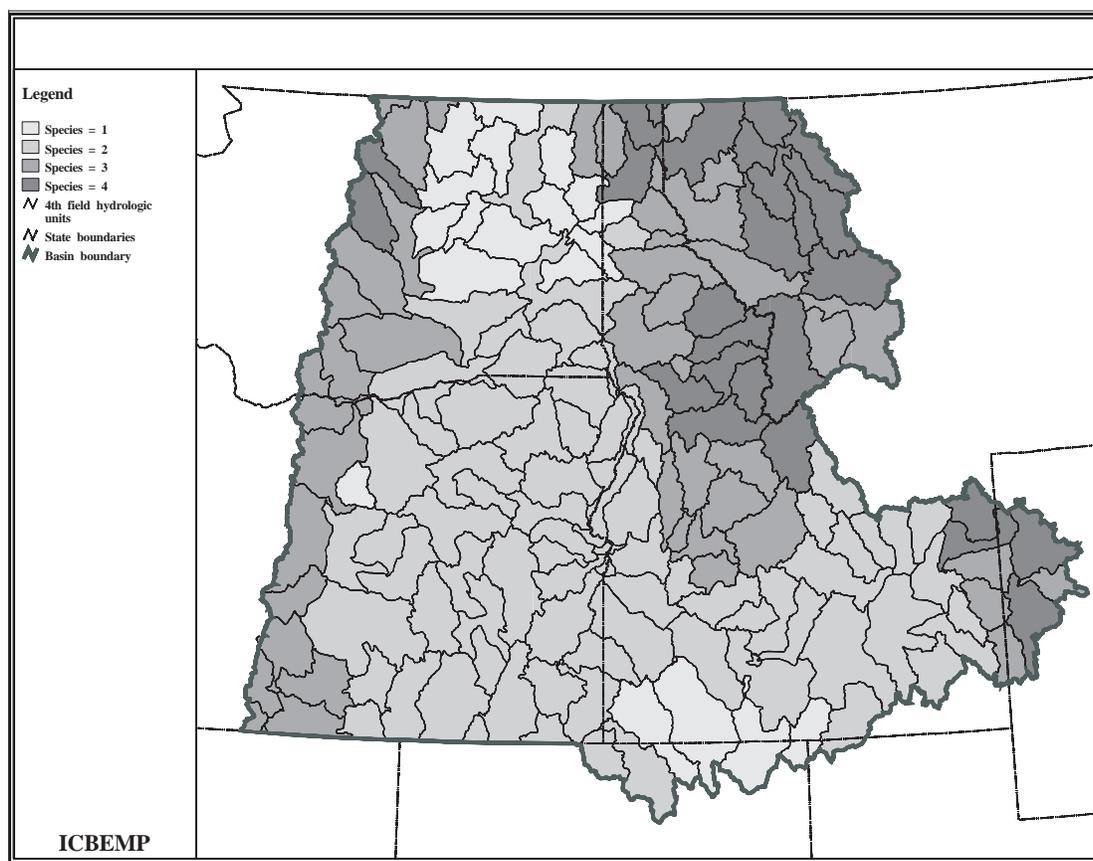
Figure 44—Numbers of threatened or endangered vertebrate species by 4th-code hydrologic unit in the basin assessment area (see table 11 for list of species). Asterisks refer to HUCs with wintering bald eagles: * = at least four threatened or endangered vertebrate species including wintering bald eagles, ** = three threatened or endangered vertebrate species including wintering bald eagles.
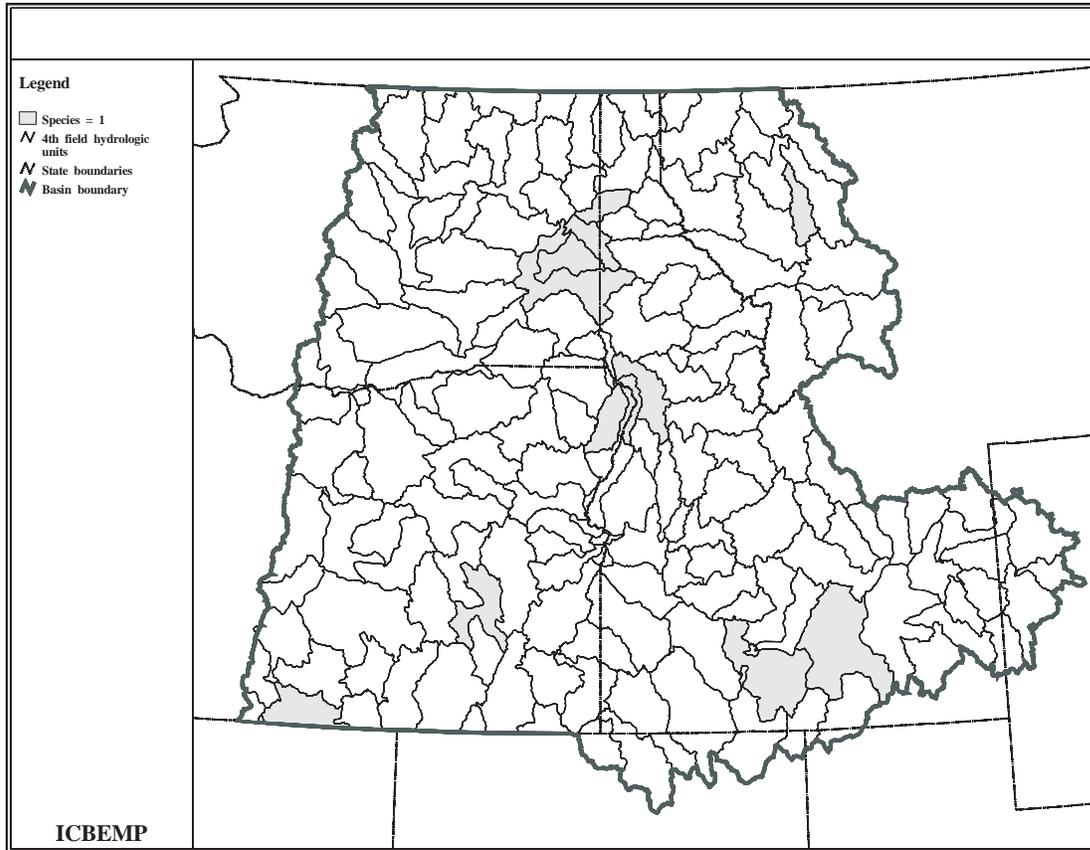
Figure 45—Numbers of threatened or endangered plant species by 4th code HUC in the basin assessment area (see table 12 for list of species).

Table 12—Threatened (T) or endangered (E) plants of the basin assessment area[a]

Species code	Scientific name	Status
ASTAPP	*Astragalus applegatei*	E
HOWAQU	*Howellia aquatilis*	T
MIRMAC	*Mirabilis macfarlanei*	E
STEMAL	*Stephanomeria malheurensis*	E

[a] Also, Ute ladies tresses (*Spiranthes diluvialis*), a federally listed threatened species, was discovered within the basin assessment area August 1996, too late to be included in the analyses in this report.

Table 13—Locally endemic vertebrates of the basin assessment area

Species code	Scientific name	Common name
DICATE	*Dicamptodon aterrimus*	Idaho giant salamander
MICPEK	*Microtus pensylvanicus kincaidi*	Potholes meadow vole
PLELAR	*Plethodon larselli*	Larch Mountain salamander
SPEWAS	*Spermophilus washingtoni*	Washington ground squirrel
THOTLI	*Thomomys talpoides limosus*	White salmon pocket gopher
TYMPHC	*Tympanuchus phasianellus columbianus*	Columbian sharp-tailed grouse
CENURO	*Centrocercus urophasianus*	Sage grouse
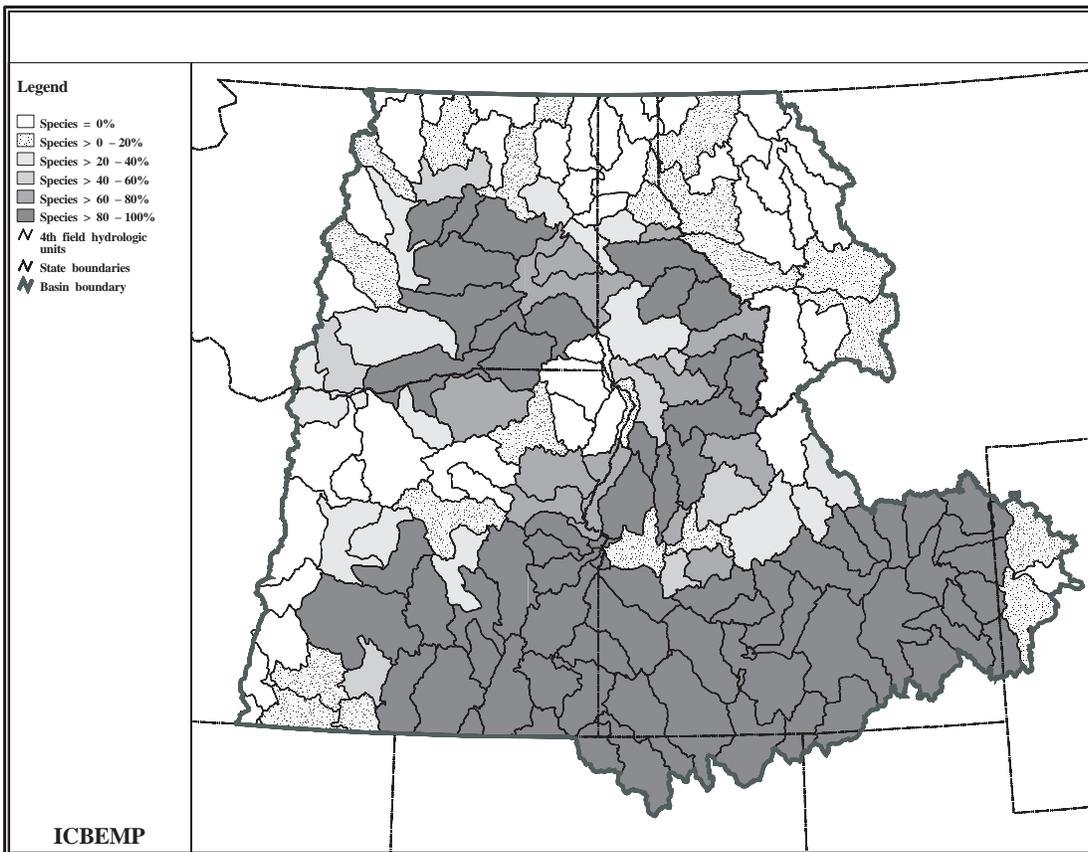
Figure 46—Percentage of all 4th-code hydrologic units in the basin assessment area that include mapped distributions of locally endemic vertebrate species (see table 13 for list of species).

Heritage Program of The Nature Conservancy)—Plants listed in the Natural Heritage databases were considered of potential conservation concern for this component. Some 129 rare plant species were included in the mapping of this component (table 14). The list was generated by (a) compiling all Heritage Program reports of species of all taxonomic groups from all locations and states overlapping the basin assessment area, (b) extracting only those reports of plant species within the basin assessment area boundary, and (c) cross-indexing the scientific names with those identified by the Science Integration Team's plant expert panels, as rare, candidate, threatened, endangered, or of special conservation concern. Data included are element occurrences of recent past collections and current locations of plants; thus, the map does not reflect just presence of these species at the immediate present, but also recent past occurrences as well. The database and map for this component show the numbers of rare plant species by 4th code HUC (fig. 47). The greatest numbers of rare plants occur in eight disjunct locations in the basin assessment area: the Cascade Range in central Washington, the southern Washington-Idaho border, the Blue Mountains of northeast Oregon, the Hell's Canyon region of the Oregon-Idaho border, central Idaho mountains, Owyhee Uplands of Oregon and Idaho, the Cascade Range of central Oregon, and the Klamath Basin of Oregon.

Component (1f): Distribution of candidate category C1 and C2 vertebrate species—Some 39 vertebrate species with candidate listing status occur in the basin assessment area (table 15). Distribution range maps were available for 28 of these species.[12] The database and map show numbers of candidate vertebrate species by 4th code HUC (fig. 48). Candidate vertebrate species are more numerous along the Cascade Range in central Washington, southeastern Washington into Idaho, the Columbia Gorge, the Cascade Range in central and southern Oregon, the Klamath Basin, the high desert area along the northeastern border of Oregon and Idaho, and the Greater Yellow Ecosystem in northwestern Wyoming and southeastern Idaho.

Habitat connectivity along the Cascade Range—Another aspect of describing ecological integrity is identifying broad-scale connectivity of habitats for vertebrates. We assumed that connectivity may be useful for maintaining well-distributed populations and viability of vertebrates. In the basin assessment area, broad-scale habitat corridors were identified by overlaying range distributions of vertebrates species. We identified potential broad-scale habitat corridors as those 4th-code HUCs that meet the following criteria: (1) the HUCs all contained the same vegetation communities, such as montane forest; (2) the HUCs all provided for distribution of vertebrates that do not occur elsewhere throughout the basin assessment area; and (3) more than two contiguous HUCs pertain to the first two criteria (thus, disjunct HUCs do not qualify, and conditions met for only one or two contiguous HUCs constitute a corridor at a finer scale of resolution than addressed in this broad-scale assessment).

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[12] At the time of this analysis, ranges for only 28 species were available. Subsequently, ranges for all 39 have been mapped and are available.

Table 14—Rare plants of the basin assessment area as listed in Natural Heritage databases

Species code	Scientific name
ALLAAS	*Allium aaseae*
ALLANC	*Allium anceps*
ALLCON	*Allium constrictum*
ALLDIC	*Allium dictuon*
ALLMAD	*Allium madidum*
ALLROB	*Allium robinsonii*
AMSCAR	*Amsinckia carinata*
ANTARC	*Antennaria arcuata*
ANTARO	*Antennaria aromatica*
ARAFEC	*Arabis fecunda*
ASTJES	*Aster jessicae*
ASTMOL	*Aster mollis*
ASTANS	*Astragalus anserinus*
ASTAPP	*Astragalus applegatei*
ASTCOL	*Astragalus columbianus*
ASTHOW	*Astragalus howellii*
ASTMUL	*Astragalus mulfordiae*
ASTONI	*Astragalus oniciformis*
ASTPAY	*Astragalus paysonii*
ASTPEC	*Astragalus peckii*
ASTSCA	*Astragalus scaphoides*
ASTSIN	*Astragalus sinuatus*
ASTSTE	*Astragalus sterilis*
ASTTEG	*Astragalus tegetarioides*
ASTTYG	*Astragalus tyghensis*
ASTYOW	*Astragalus yoder-williamsii*
BALROS	*Balsamorhiza rosea*
BOTASC	*Botrychium ascendens*
BOTCRE	*Botrychium crenulatum*
BOTLUN	*Botrychium lunaria*
BOTPAR	*Botrychium paradoxum*
BOTPED	*Botrychium pedunculosum*
BOTPUM	*Botrychium pumicola*
CALNIT	*Calochortus nitidus*

Table 14—Rare plants of the basin assessment area as listed in Natural Heritage databases (continued)

Species code	Scientific name
CASCHL	*Castilleja chlorotica*
CASCHR	*Castilleja christii*
CASCRY	*Castilleja cryptantha*
CASFRA	*Castilleja fraterna*
CASRUB	*Castilleja rubida*
CHACUS	*Chaenactis cusickii*
COLMAZ	*Collomia mazama*
COLREN	*Collomia renacta*
CYMDAV	*Cymopterus davisii*
CYMDOU	*Cymopterus douglassii*
CYMNIV	*Cymopterus nivalis*
CYPFAS	*Cypripedium fasciculatum*
DELVIR	*Delphinium viridescens*
DESTOR	*Descurainia torulosa*
DOUIDA	*Douglasia idahoensis*
DRATRI	*Draba trichocarpa*
ERIBAS	*Erigeron basalticus*
ERILAC	*Erigeron lackschewitzii*
ERISAL	*Erigeron salmonensis*
ERICHR	*Eriogonum chrysops*
ERICRO	*Eriogonum crosbyae*
ERICUS	*Eriogonum cusickii*
ERIMEL	*Eriogonum meledonum*
ERIPRO	*Eriogonum prociduum*
GRAHET	*Gratiola heterosepala*
GRIHOW	*Grindelia howellii*
HACCRO	*Hackelia cronquistii*
HACVEN	*Hackelia venusta*
HAPINS	*Haplopappus insecticruris*
HAPLIA	*Haplopappus liatriformis*
HAPRAD	*Haplopappus radiatus*
HOWAQU	*Howellia aquatilis*
ILILON	*Iliamna longisepala*

Table 14—Rare plants of the basin assessment area as listed in Natural Heritage databases (continued)

Species code	Scientific name
LEPDAV	*Lepidium davisii*
LEPGLA	*Leptodactylon glabrum*
LESHUM	*Lesquerella humilis*
LESPAY	*Lesquerella paysonii*
LOMERY	*Lomatium erythrocarpum*
LOMGRE	*Lomatium greenmanii*
LOMSUK	*Lomatium suksdorfii*
LOMTUB	*Lomatium tuberosum*
LUISER	*Luina serpentina*
LUPCUS	*Lupinus cusickii*
MECORE	*Meconella oregana*
MENMOL	*Mentzelia mollis*
MENPAC	*Mentzelia packardiae*
MIMCLI	*Mimulus clivicola*
MIMHYM	*Mimulus hymenophyllus*
MIMJEP	*Mimulus jepsonii*
MIMJUN	*Mimulus jungermannioides*
MIMLAT	*Mimulus latidens*
MIMPAT	*Mimulus patulus*
MIMPUL	*Mimulus pulsiferae*
MIMPYG	*Mimulus pygmaeus*
MIMSUK	*Mimulus suksdorfii*
MIMTRI	*Mimulus tricolor*
MIRMAC	*Mirabilis macfarlanei*
MUSLIN	*Musineon lineare*
OENPSA	*Oenothera psammophila*
ORYCON	*Oryzopsis contracta*
ORYHEN	*Oryzopsis hendersonii*
PAPPYG	*Papaver pygmaeum*
PENBAR	*Penstemon barrettiae*
PENCOM	*Penstemon compactus*
PENGLA	*Penstemon glaucinus*
PENIDA	*Penstemon idahoensis*

Species code	Scientific name
PENJAN	*Penstemon janishiae*
PENLEM	*Penstemon lemhiensis*
PENPEC	*Penstemon peckii*
PERERY	*Perideridia erythrorhiza*
PHAINC	*Phacelia inconspicua*
PHALEN	*Phacelia lenta*
PHAMIN	*Phacelia minutissima*
PHLIDA	*Phlox idahonis*
PLEORE	*Pleuropogon oregonus*
POLPEC	*Polemonium pectinatum*
POTCOT	*Potentilla cottamii*
PRIALC	*Primula alcalina*
RANREC	*Ranunculus reconditus*
RORCOL	*Rorippa columbiae*
RUBBAR	*Rubus bartonianus*
RUBNIG	*Rubus nigerrimus*
SENERT	*Senecio ertterae*
SILSEE	*Silene seelyi*
SILSPA	*Silene spaldingii*
SISSAR	*Sisyrinchium sarmentosum*
STEMAL	*Stephanomeria malheurensis*
TAUHOO	*Tauschia hooveri*
TEXSAJ	*Texosporium sancti-jacobi*
THEEUC	*Thelypodium eucosmum*
THEREP	*Thelypodium repandum*
TRIDOU	*Trifolium douglasii*
TRILEI	*Trifolium leibergii*
TRIOWY	*Trifolium owyheense*
TRITHO	*Trifolium thompsonii*
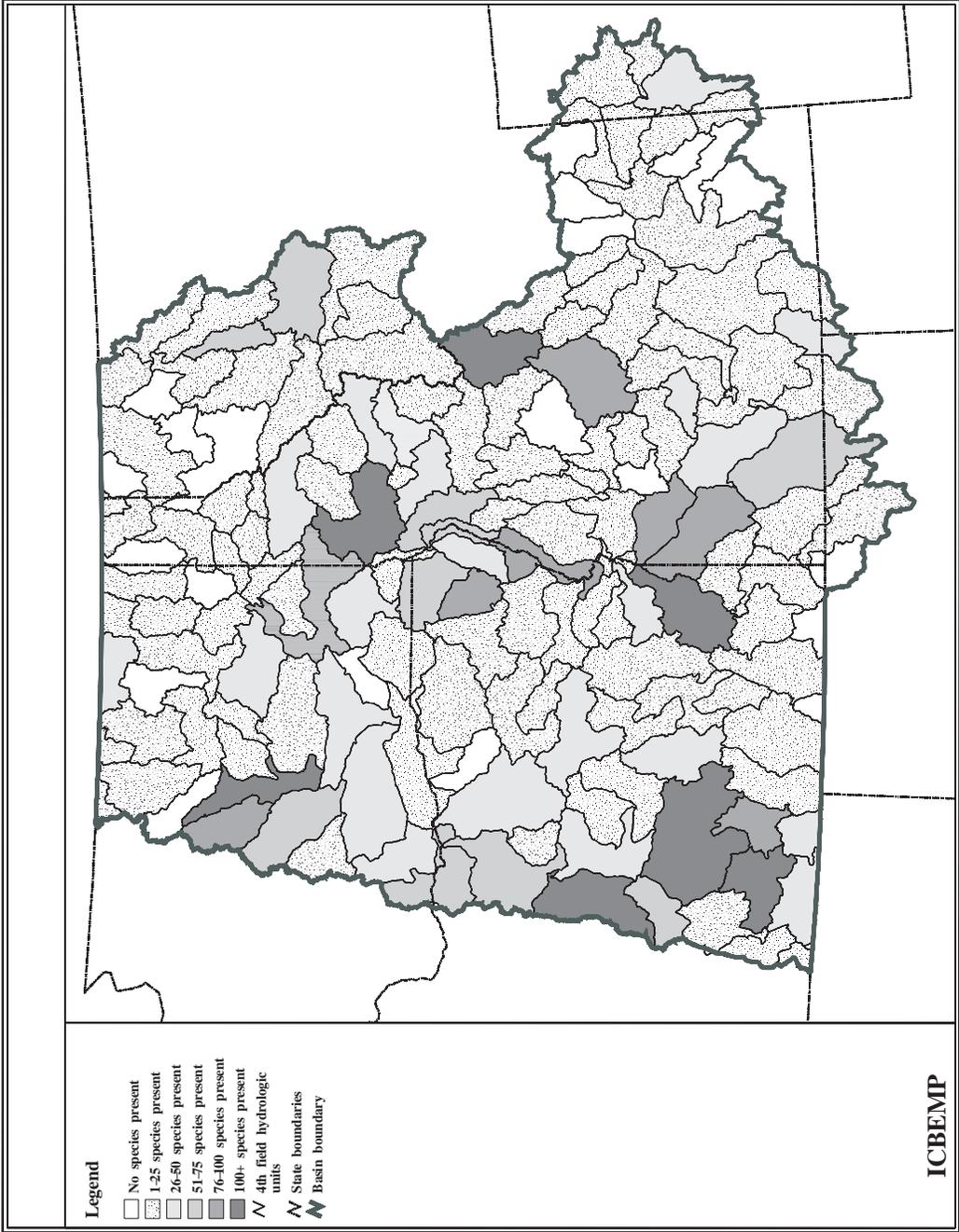
Figure 47—Numbers of rare plants (as identified in Natural Heritage databases from the Heritage Program or similar state programs of The Nature Conservancy) by 4th-code hydrologic unit in the basin assessment area (see table 17 for list of species).

Legend

No species present
1-25 species present
26-50 species present
51-75 species present
76-100 species present
100+ species present

N 4th field hydrologic units
N State boundaries
N Basin boundary

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Table 15—Federally listed candidate category C1 or C2 vertebrates of the basin assessment area[a]

Species code	Scientific name	Common name
ACCGEN	*Accipiter gentilis*	Northern goshawk\a
AGETRI	*Agelaius tricolor*	Tricolored blackbird
ASCTRU	*Ascaphus truei*	Tailed frog
ATHCUN	*Athene cunicularia*	Burrowing owl
BRAIDA	*Brachylagus idahoensis*	Pygmy rabbit
BUFBOR	*Bufo boreas*	Western toad
BUTREG	*Buteo regalis*	Ferruginous hawk
CENURO	*Centrocercus urophasianus*	Sage grouse
CHLNIG	*Chlidonias niger*	Black tern
CLEMAR	*Clemmys marmorata*	Western pond turtle\b
CONBOR	*Contopus borealis*	Olive-sided flycatcher
CYGBUC	*Cygnus buccinator*	Trumpeter swan
EMPTRA	*Empidonax traillii*	Willow flycatcher\a
EUDMAC	*Euderma maculatum*	Spotted bat
GULGUL	*Gulo gulo*	Wolverine\b
HISHIS	*Histrionicus histrionicus*	Harlequin duck
IXOEXH	*Ixobrychus exilis hesperis*	Western least bittern
LANLUD	*Lanius ludovicianus*	Loggerhead shrike
LYNLYN	*Lynx lynx*	Lynx\b
MARPEN	*Martes pennanti*	Fisher\b
MICPKI	*Microtus pennsylvanicus kincaidi*	Potholes meadow vole
MYOCIL	*Myotis ciliolabrum*	Western small-footed myotis\a
MYOEVO	*Myotis evotis*	Long-eared myotis\a
MYOTHY	*Myotis thysanodes*	Fringed myotis
MYOVOL	*Myotis volans*	Long-legged myotis\a
MYOYUM	*Myotis yumanensis*	Yuma myotis
OVICCA	*Ovis canadensis californiana*	California bighorn sheep\b
PLECHI	*Plegadis chihi*	White-faced ibis\a
PLELAR	*Plethodon larselli*	Larch mountain salamander
PLETOW	*Plecotus townsendii pallescens*	Pale western big-eared bat
RANAUR	*Rana aurora*	Red-legged frog
RANCAS	*Rana cascadae*	Cascades frog
RANLUT	*Rana luteiventris*	Spotted frog
SCEGRA	*Sceloporus graciosus graciosus*	Sagebrush lizard
SORPRE	*Sorex preblei*	Preble's shrew
SPEBRE	*Spermophilus brunneus*	Idaho ground squirrel
SPEWAS	*Spermophilus washingtoni*	Washington ground squirrel
TYMPHC	*Tympanuchus phasianellus columbianus*	Columbian sharp-tailed grouse

[a] See footnote 11 chapter 4 for recent changes in candidate species listings by USDI Fish and Wildlife Service. At the time of this analysis, only 28 species' ranges were available. (Subsequently, all 39 species' ranges were mapped and are available.) The remaining 11 species are marked as \a -scarce but ubiquitous or widespread in the basin assessment area or \b - not ubiquitous but for which no range map was available for the entire basin assessment area.
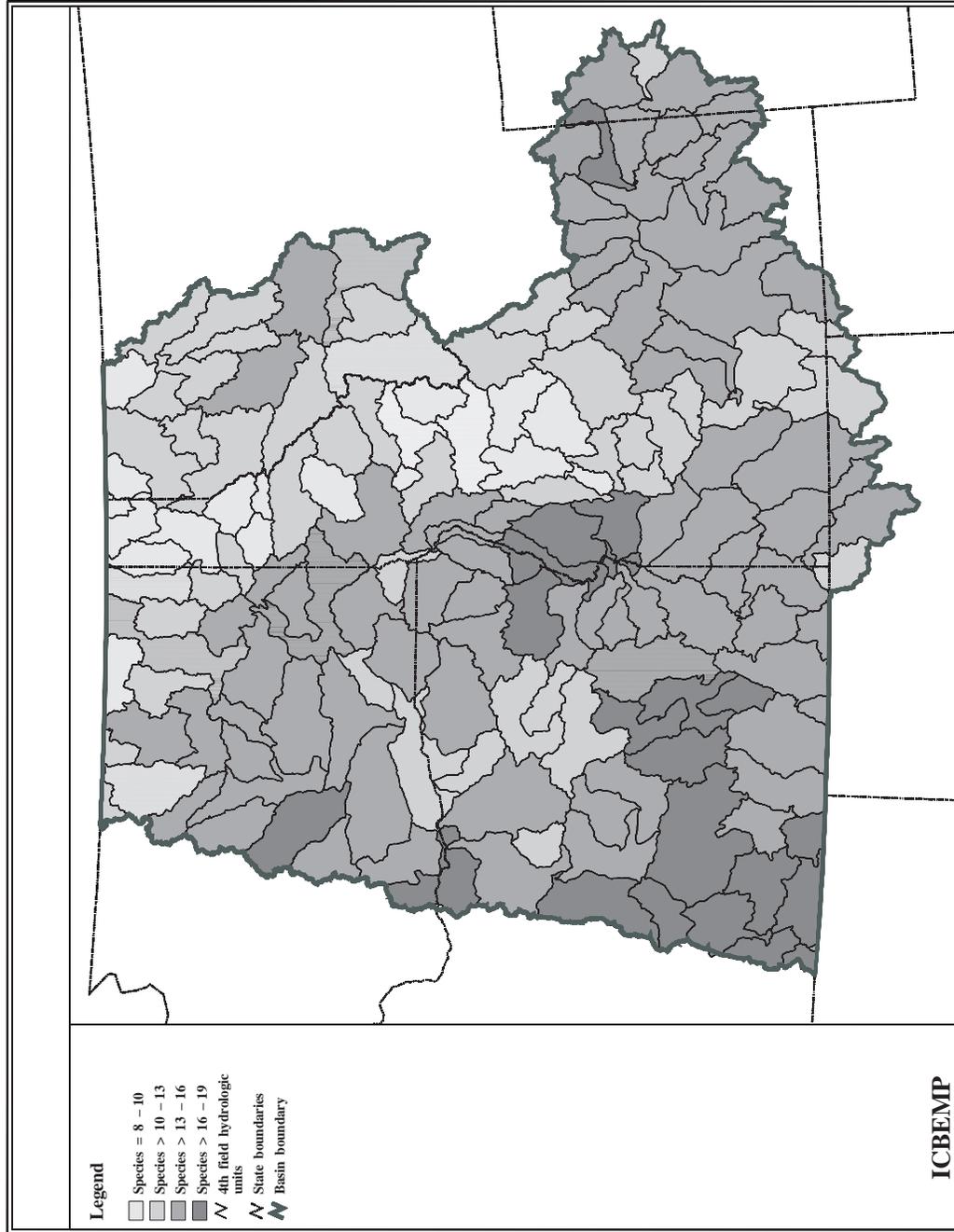
Figure 48—Numbers of federally listed candidate category C1 or C2 vertebrate species by 4th-code hydrologic unit in the basin assessment area (see table 15 for list of species, and text footnote 11 for explanation of recent changes in the candidate species listing).

Although some potential vertebrate habitat corridors could be identified—such as linking Glacier National Park with Yellowstone National Park, or the Blue Mountains and the central Idaho mountains, for many montane or alpine species including mustelids—they did not meet the second criterion for this particular component of being the only locations of associated vertebrate species within the basin assessment area. They are included, however, in the "Full Trophic Ladder Component," 3(h), discussed below. The following integrity component relates to habitat connectivity as defined above.

Component (1d):[13] Distribution of species occurring along key habitat corridors—One major habitat corridor that met all the above criteria was found along the eastern spine of the Cascade Range. An assemblage of seven vertebrates[14] (table 16) occurs in the basin assessment area only along the spine or eastern flanks of the Cascade Range in Washington and Oregon collectively delineate a mid- to high-elevation montane corridor. The database and map show presence of this corridor by 4th code HUC (fig. 49). The corridor occurs along the eastern flanks of the Cascade Range; additional 4th code HUCs in eastern Washington, northern Idaho, and western Montana also contain disjunct populations of these species and are indicated on the map.

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[13] This component is numbered out of sequence here to remain consistent with the map index codes on record for ICBEMP.

[14] An additional, eighth species fitting these criteria is mountain beaver (*Aplodontia rufa*), which was not mapped in time for this analysis. Its inclusion would not alter the results, as its distributional range within the basin assessment area matches that of the other species listed for this component. Other vertebrate species such as northwestern salamander, Cope's giant salamander, ensatina (*Ensatina eschscholtzii*), Larch Mountain salamander, Columbian black-tailed deer (*Odocoileus hemionus columbianus*), and others also occur within the basin assessment area only in the Cascade Range, but not broadly along the spine or eastern front.

Ecological Integrity Goal 2: Maintain Long-Term Evolutionary Potential of Species

The overall concept of maintaining long-term evolutionary potential of species entails, in part, maintaining unique ranges and centers of biodiversity, rarity, and endemism.

Species components—The following integrity component relates to distribution of species that may be critical to maintaining long-term evolutionary potential. Other species components to help meet this goal include maintaining unique ecotypes of species, maintaining species at the periphery of their global range, and maintaining unique subspecies, varieties, or phenotypes (Marcot and others 1996). These additional components were not available for mapping in this analysis.

Component (2a): Distribution of disjunct vertebrate species populations—Managing for disjunct populations of plants and animals is an important facet of maintaining genetic diversity and longterm evolutionary potential of species (Kruckeberg and Rabinowitz 1985, Millar and Libby 1991).

Some 11 vertebrate species are coded in the SER database as having disjunct ranges within the basin assessment area. Two of these species, however, Virginia opossum (*Didelphis virginiana*) and bullfrog (*Rana catesbeiana*), are mainly recent invaders or introduced, are not of conservation concern, and are not included in this analysis. In fact, bullfrogs, widely introduced to ponds and lakes throughout the basin assessment area, are predators on some of the more increasingly scarce native amphibians such as red-legged frog. A third species with a disjunct range, pygmy shrew (*Sorex hoyi*), is largely contiguous within the basin assessment area (as mapped at the broad scale used by the expert panels for this project) with only a small portion of its range disjunct, so it

Table 16—Vertebrates that occur within the basin assessment area only along a broad latitudinal extent of the eastern flanks of the Cascade Range[a]

Species code	Scientific name	Common name
RANCAS	*Rana cascadae*	Cascades frog
TARGRA	*Taricha granulosa*	Rough skinned newt
STROCA	*Strix occidentalis caurina*	Northern spotted owl
SORTRO	*Sorex trowbridgii*	Trowbridge's shrew
NEUGIB	*Neurotrichus gibsii*	Shrew mole
SPESAT	*Spermophilus saturatus*	Cascade golden mantled ground squirrel
ZAPTRI	*Zapus trinotatus*	Pacific jumping mouse

[a] These include species that might benefit by latitudinal habitat corridors of montane and subalpine forests along the eastern slope of the Cascade Range. This list does not include species that enter the basin assessment area from the west only at one point across the spine of the Cascade Range or only up the Columbia River Gorge.
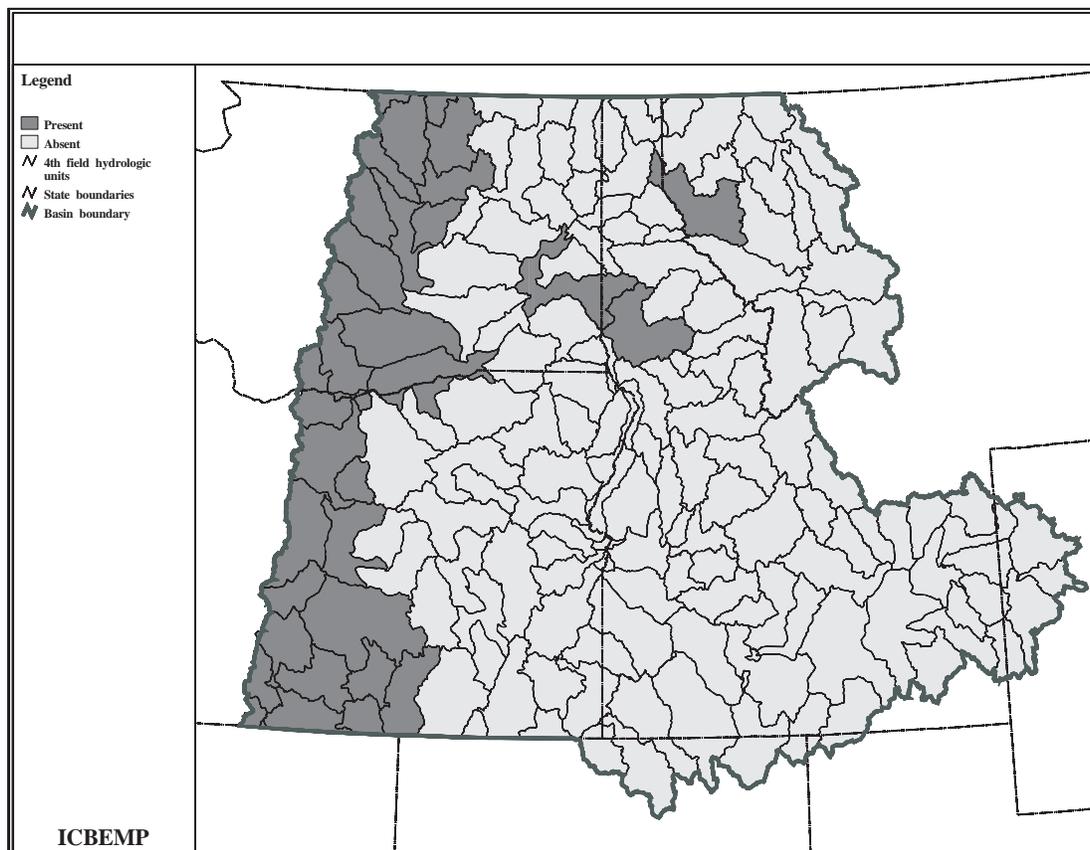
Figure 49—Occurrence of a habitat corridor for vertebrates of the Cascade Range by 4th-code hydrologic unit in the basin assessment area (see text for further explanation of the extraneous hydrologic units shown shaded here).

was excluded from subsequent analyses. The remaining eight species with disjunct ranges within the assessment area are included in the analyses (table 17). Note that some of these eight species also may occur in one of the components listed above (for example, whooping crane (*Grus americana*) is also an endangered species). Wild turkey (*Meleagris gallopavo*) was included in this list because, although its disjunct populations result from introductions, the species has naturalized in these ranges (it is a "desired nonnative vertebrate" in the parlance of National Forest Management Act Regulations 38 CFR 219) and is a sought-after species of positive economic and social importance. The database and map for this component show percentage of the area of each 4th code HUC with coverage by any or all of these species (fig. 50). A count of species by 4th code HUC was not used as the measure because, interestingly, many of these species are distributed as allopatric (nonoverlapping ranges), so that a simple count of species by HUC was not a sensitive measure of distribution. The mapped results suggest that HUCs important to disjunct vertebrate populations occur in Montana, northern Idaho, central Idaho mountains, Snake River plain in southwest Idaho, along the Washington-Oregon border, and in the Cascade Range in Oregon eastward into the high desert and Klamath Basin.

Diversity components—Component (2b): Mapped locations of biodiversity hot spots (of plants and animals combined)—This theme was derived by overlaying the maps of centers of concentration of biodiversity of plants and animals (component 2d, below) and generating polygons where at least three centers overlap (see Marcot and others 1997 for further information on conditions within each hot spot). The database and map for this component show percentage of the area of each 4th code HUC with coverage by any or all polygons of biodiversity hot spots (fig. 51). Seven biodiversity hot spots were identified in various locations throughout the basin assessment area.

Component (2c): Mapped locations of species rarity and endemism hot spots (of plants and animals combined)—This theme was derived by overlaying the maps of centers of concentration of species rarity and endemism of plants and animals (component 2d, below), and generating polygons where at least three centers overlap (see Marcot and others 1997 for further information on conditions within each hot spot). The database and map show percentage of the area of each 4th code HUC with coverage by any or all polygons (fig. 52). Twelve hot spots of species rarity and endemism were identified in various locations, mostly in southern Washington, in Oregon, and southwestern Idaho. One major concentration area is the Columbia River Gorge.

Component (2d): Mapped locations of centers of concentration of biodiversity, and of species rarity and endemism (for plants and animals combined)—This theme was derived as polygons mapped by expert panels during the panel meeting on natural areas (see Marcot and others 1997 for further information on methods). The database and map show percentage of the area of each 4th code HUC with coverage by any or all polygons (fig. 53). Collectively, centers of concentration for plants and animals occur in many locations throughout the basin assessment area.

Ecological integrity goal 3: manage for multiple ecological domains and evolutionary timeframes

The overall concept of managing for multiple ecological domains and evolutionary timeframes entails ensuring that unique species assemblages by geographic area are recognized and provided for, and that the full trophic ladder occurs (represented here by distributions of large vertebrate carnivores). Other components of this goal also may entail ensuring that the full range of historic and current habitat conditions and terrestrial communities are provided, including mid-scale and site-specific microhabitats and substrates; however, these components were not mapped for this analysis.

Table 17—Examples of vertebrate species with disjunct distributions in the basin assessment area, as mapped at the broad scale

Species code	Scientific name	Common name
BUFWOO	*Bufo woodhousii*	Woodhouse's toad
GRUAME	*Grus ameriana*	Whooping crane
LAMZON	*Lampropeltis zonata*	California mountain kingsnake
MELGAL	*Meleagris gallopavo*	Wild turkey
RANCLA	*Rana clamitans*	Green frog
RANSYL	*Rana sylvatica*	Wood frog
RHILEC	*Rhinocheilus lecontei*	Longnose snake
SONSEM	*Sonora semiannulata*	Ground snake
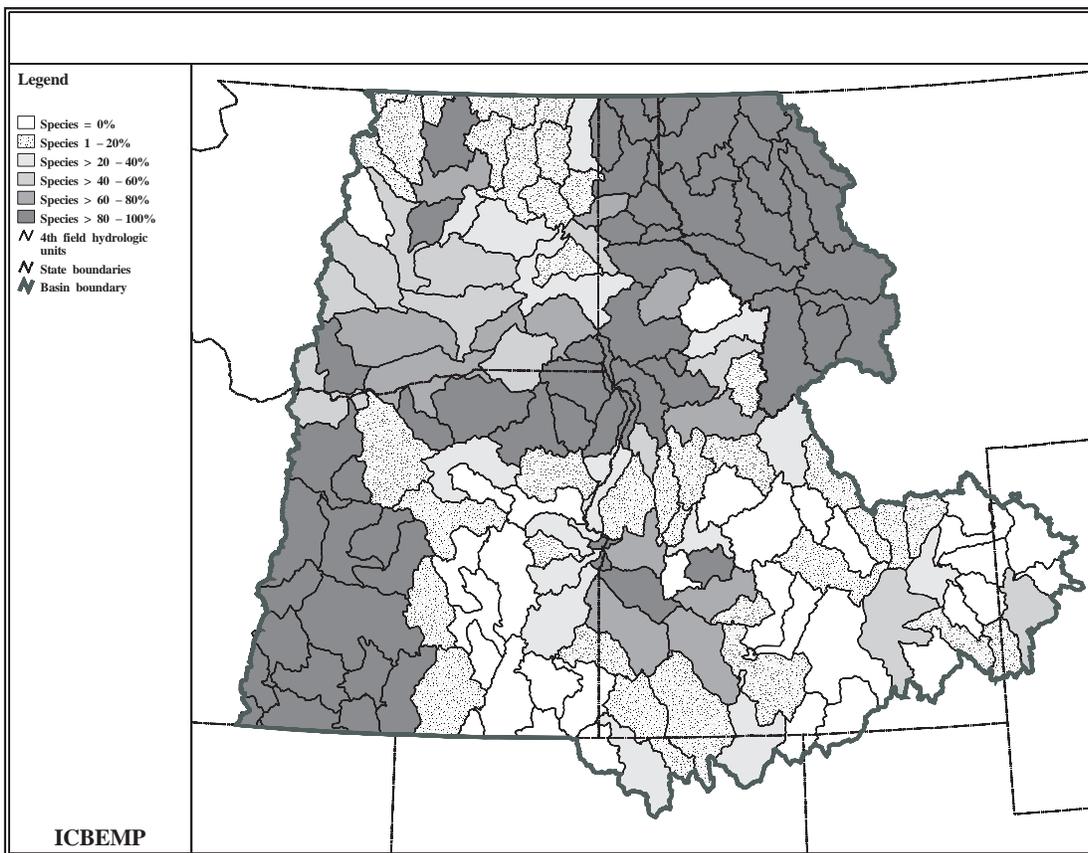
Figure 50—Percentage of each 4th-code hydrologic unit in the basin assessment area that includes mapped distributions of vertebrate species with disjunct populations (see table 17 for list of species).
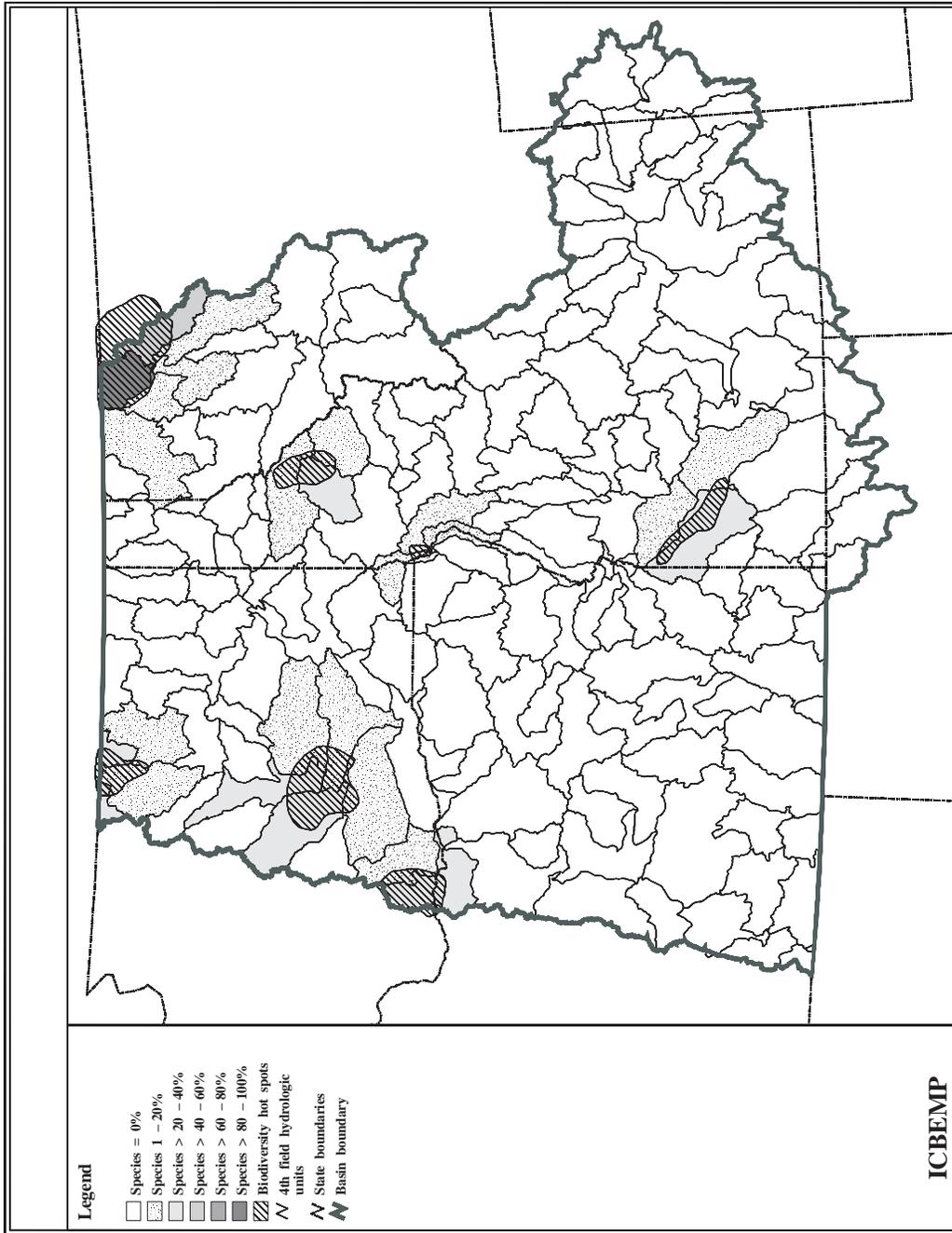
Figure 51—Percentage of each 4th-code hydrologic unit in the basin assessment area that includes biodiversity hot spots of plants and animals (source: Marcot and others 1997).
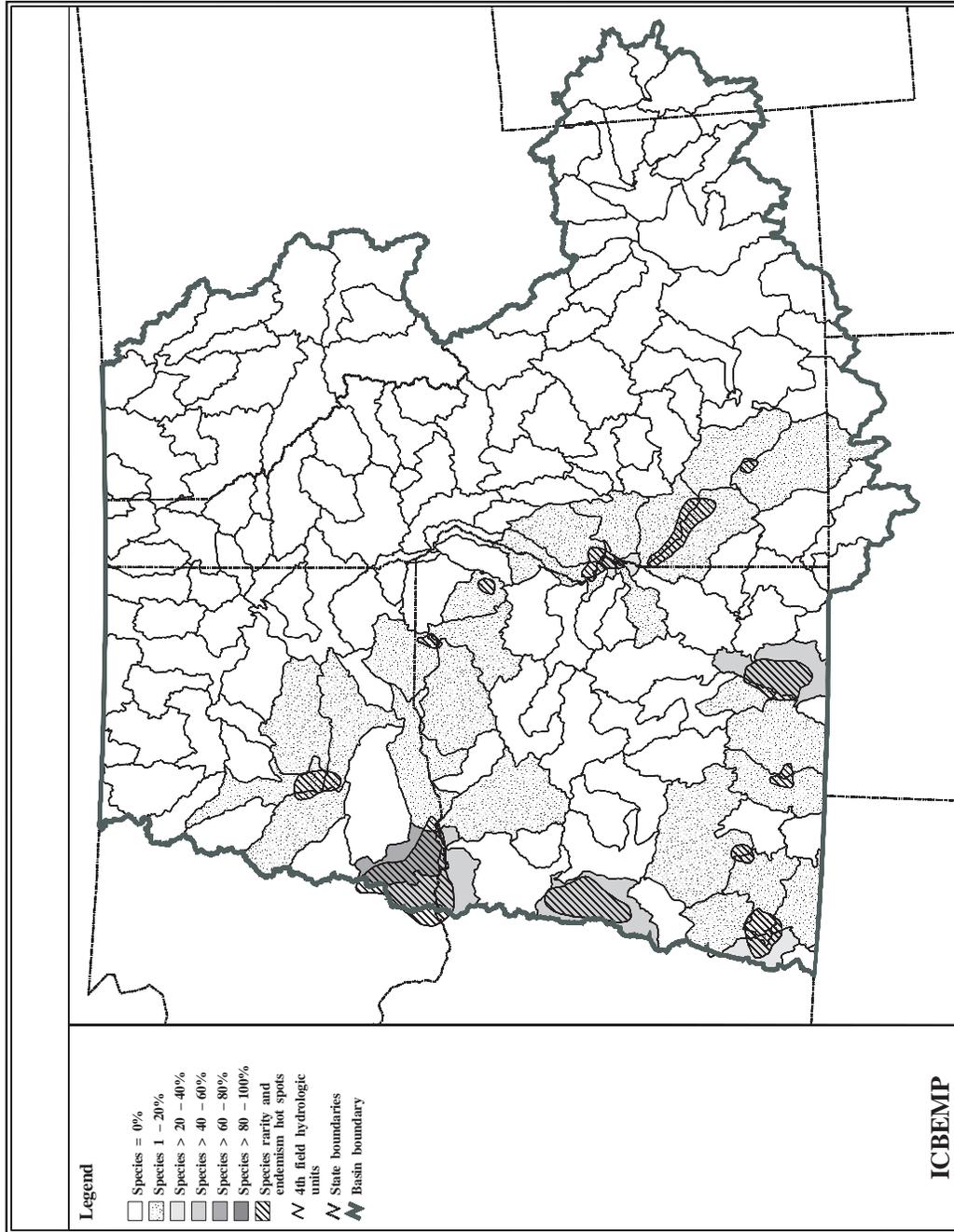
Figure 52—Percentage of each 4th-code hydrologic unit in the basin assessment area that includes species rarity and endemism hot spots of plants and animals (source: Marcot and others 1997).
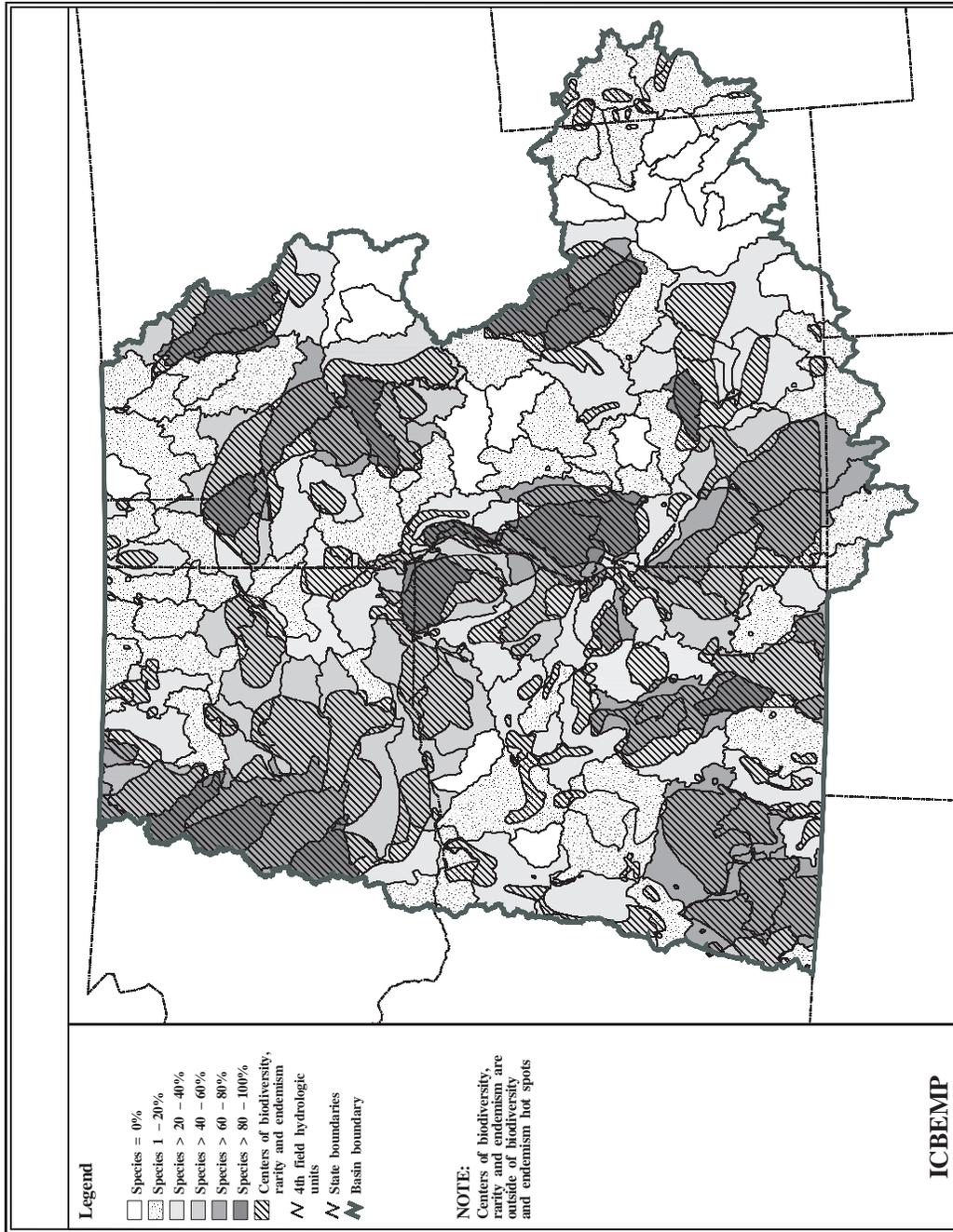
Figure 53—Percentage of each 4th-code hydrologic unit in the basin assessment area that includes centers of concentration of biodiversity, or of species rarity and endemism, of plants and animals (source: Marcot and others 1997).

Unique species assemblage components—The following integrity components relate to identifying unique vertebrate species assemblages by geographic area (ERU), as identified and listed in Marcot and others (1997).[15] Many of these assemblages are of species that occur peripherally in the basin assessment area. Managing for the periphery of ranges of species can be important for maintaining long-term evolutionary potential (Furlow and Armijo-Prewitt 1995, Kruckeberg and Rabinowitz 1985, Lesica and Allendorf 1995), for it is at the edges of ranges where environmental factors often differ the most and new genotypes and phenotypes emerge (see Marcot and others 1997 for examples in the basin assessment area).

Component (3a): Upper Klamath Basin species—We identified a set of 10 species that are closely associated with the Upper Klamath Basin ERU in southern Oregon (fig. 54). The database and map show number of species by 4th code HUC.

Component (3b): Owyhee Upland species—We identified a set of nine species that are closely associated with the Owyhee Upland ERU in southern Oregon and Idaho (fig. 55). The database and map show number of species by 4th code HUC.

Component (3c): Northern Great Basin species—We identified a set of three species that are closely associated with the northern Great Basin ERU in southern Oregon (fig. 56). The database and map show number of species by 4th code HUC.

Component (3d): Amphibians of the Columbia River Gorge—This unique assemblage consists of amphibian species that enter into the basin assessment area mainly or solely through the Columbia River Gorge (fig. 57). The database and map show number of species by 4th code HUC.

Component (3e): Snake River Headwaters ERU and western Wyoming species—A set of eight species were identified that are closely associated with the Snake River Headwaters ERU in southeastern Idaho, and the western Wyoming (Greater Yellowstone Ecosystem) region (fig. 58). The database and map show number of species by 4th code HUC.

Component (3f): Upper Snake River ERU species—Two species were identified that are closely associated with the Upper Snake River ERU in southern Idaho (fig. 59). The database and map show number of species by 4th code HUC.

Component (3g): Western Montana species—Two species were identified that are closely associated with western Montana (fig. 60). The database and map show number of species by 4th code HUC.

Full trophic ladder component—Component (3h): Vertebrate carnivores—Eight wide-ranging vertebrate carnivores occur in the basin assessment area: grizzly bear (*Ursus arctos*), black bear (*U. americanus*), gray wolf (*Canis lupus*), cougar (*Felis concolor*), lynx (*Lynx lynx*), wolverine, fisher (*Martes pennanti*), and American marten (*M. americana*). Four of these species were mapped and are included in this component (fig. 61).[16] The full set of vertebrate carnivores—and by inference, the full trophic ladder—once likely ranged throughout the entire basin assessment area, but now is present only in the northern Rocky Mountains, including Glacier National Park, Yellowstone National Park and adjacent lands, and in other locations where grizzly bear and gray wolf recovery areas overlap, as in central Idaho and north-central Washington. The database and map for this component show number of species by 4th code HUC (fig. 61).

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[15] Since the current analysis was conducted, some range maps of species have been refined, ranges of additional vertebrate species of the basin assessment area have been mapped, and additional species have been added to these lists of unique species assemblages by ERU and geographic area. The lists presented in Marcot and others (1997) reflect these additions but were not included in time to update analyses presented here. We do not anticipate, however, that these additions would qualitatively change results presented here.

[16] Since this analysis, ranges for the remaining four carnivores also were mapped. Their distributional ranges more than overlap those of the four initially mapped carnivore species. Thus, their inclusion in this analysis does not change the results of identifying centers of high-carnivore richness.
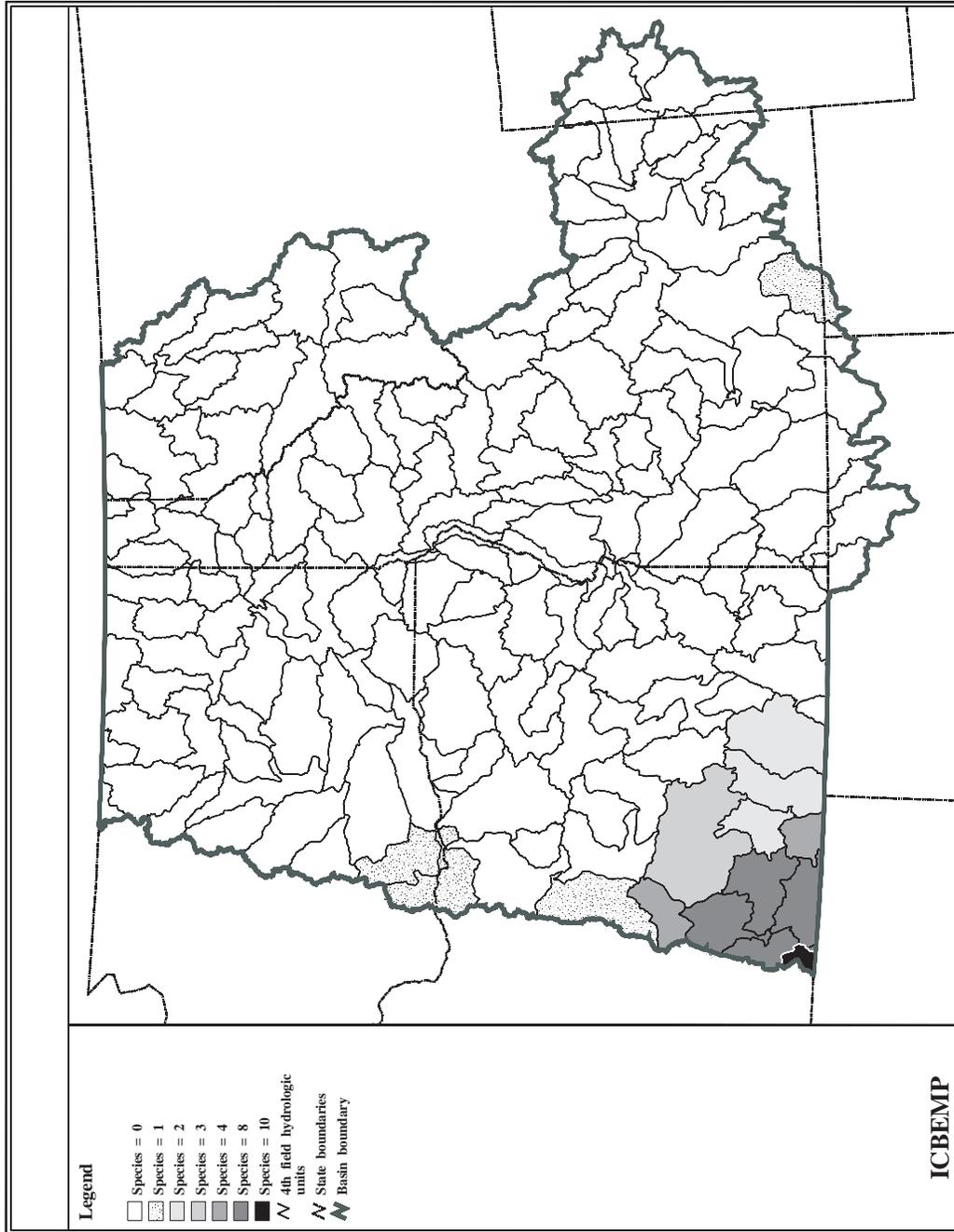
Figure 54—Numbers of species closely associated with the Upper Klamath Basin ecology reporting unit (ERU), by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species).
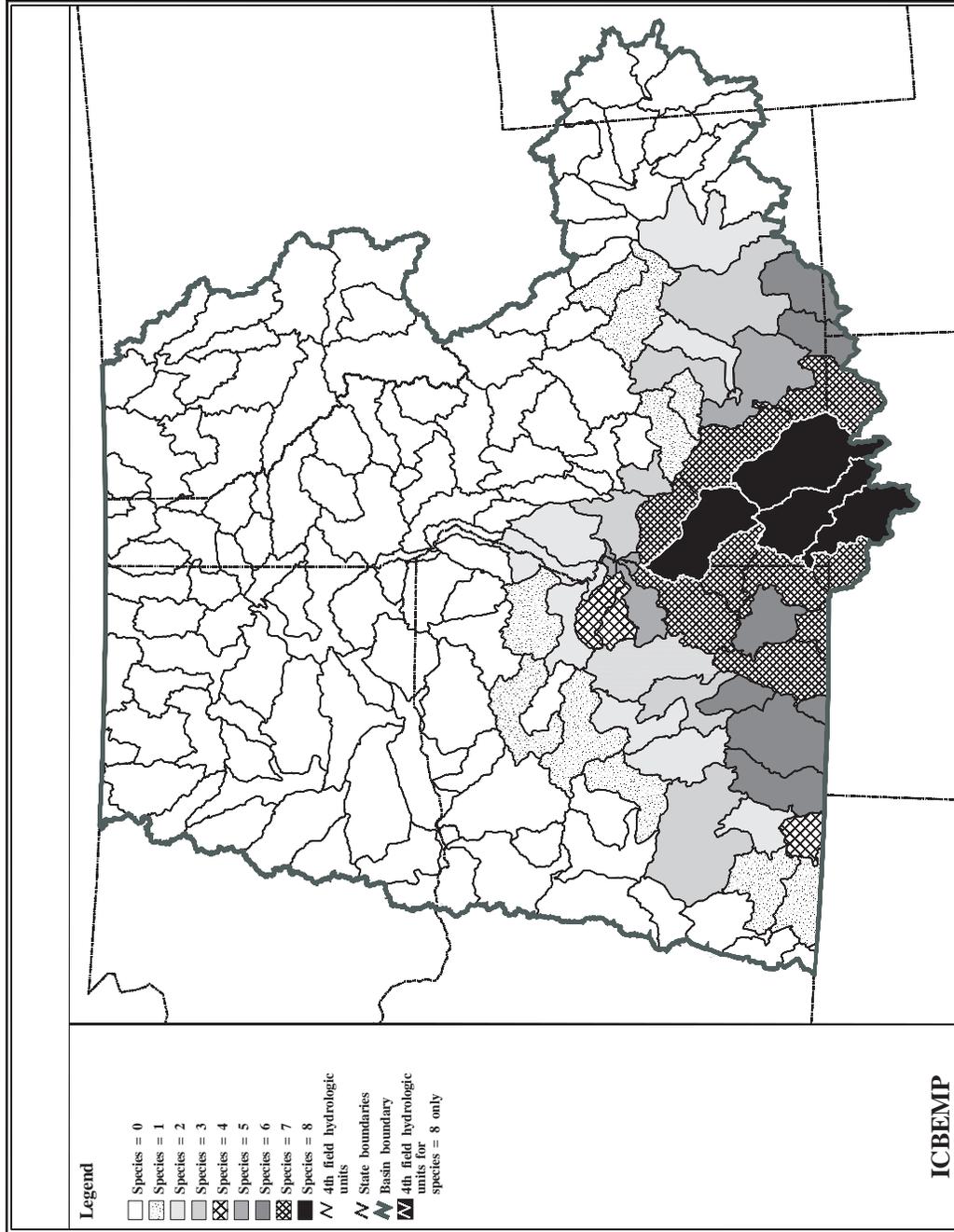
Figure 55—Numbers of species closely associated with the Owyhee Uplands ERU, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species).

Figure 56—Numbers of species closely associated with the Northern Great Basin ERU, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species).

Legend

Species = 0
Species = 1
Species = 2
Species = 3
4th field hydrologic units
State boundaries
Basin boundary

ICBEMP

Figure 57—Numbers of amphibian species closely associated with the Columbia River Gorge, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species).

Figure 58—Numbers of species closely associated with the Snake River Headwaters ERU and western Wyoming, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species.)

Figure 59—Numbers of species closely associated with the Upper Snake River ERU, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species.)

Figure 56—Numbers of species closely associated with the Northern Great Basin ERU, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species).

Legend

☐ Species = 0
☐ Species = 1
▨ Species = 2
▩ Species = 3
∿ 4th field hydrologic units
∕ State boundaries
∿ Basin boundary

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ICBEMP

Figure 57—Numbers of amphibian species closely associated with the Columbia River Gorge, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species).

Figure 58—Numbers of species closely associated with the Snake River Headwaters ERU and western Wyoming, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species.)

Figure 59—Numbers of species closely associated with the Upper Snake River ERU, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species.)

Figure 60—Numbers of species closely associated with western Montana, by 4th-code hydrologic unit in the basin assessment area (see Marcot and others 1997 for list of species.)
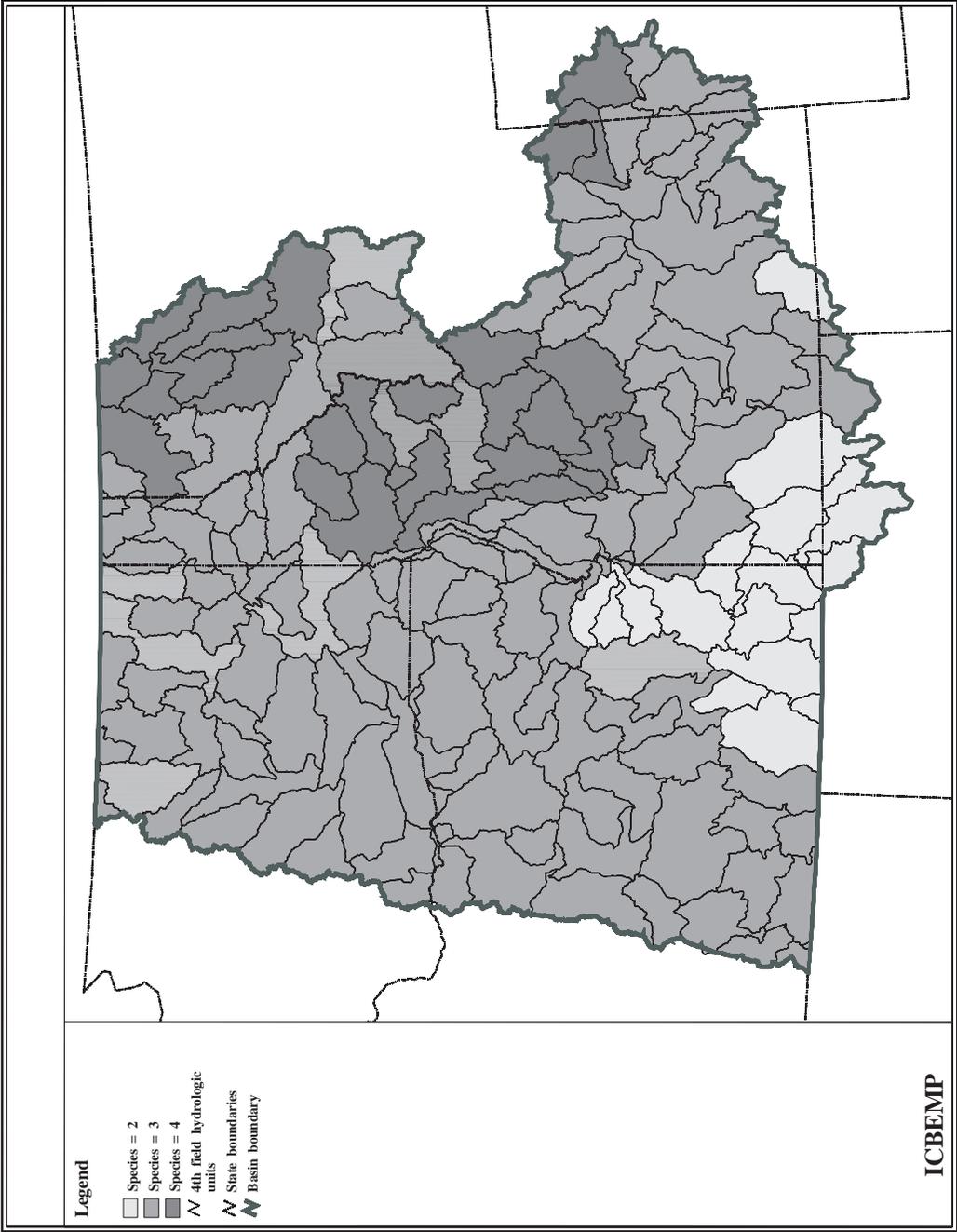
Figure 61—Numbers of wide-ranging vertebrate carnivores (gray wolf, black bear, cougar, and coyote) by 4th-code hydrologic unit in the basin assessment area (see text and Marcot and others 1997 for full list of species.) * = include gray wolf (not initially mapped).

Pictures of Terrestrial Integrity: Combining Maps for Each Goal

The final step in depicting terrestrial ecological integrity of the basin assessment area was to combine all components under each goal into maps depicting overall conditions for each of the three goals. Similarly, Lyons and others (1995) produced composite maps to depict overall integrity conditions of fish assemblages in their study. They calculated index values for sites as the sum of the scores for their integrity components. Majer and Beeston (1996) followed a similar method to depict overall biological integrity of ant assemblages in Australia.

The database created for each component above displayed conditions for each 4th code HUC in the basin assessment area. Components denoted as number of species were then normalized in the database to values ranging from 0 to 100 percent by dividing the number of species in each HUC by the total number of species possible in each assessment component and multiplying by 100. Components denoted as percentages were not changed. In this way, all components were represented in the database as percentage values within each 4th code HUC.

Then, for each of the integrity goals, all components were averaged by taking the arithmetic mean of the percentages for each 4th code HUC. The results, expressed as mean percentages in each HUC, were mapped for each of the three goals. These overall maps depict composite conditions of all components under each goal.

The overall map for goal 1, maintaining species viability, is shown in figure 62. Hydrologic unit codes with higher percentage values in this map represent locations with more threatened, endangered, endemic, rare, or candidate plants or animals, and overlap with the High Cascade Range habitat corridor. Thus, the map highlights areas that may warrant particular management attention for this goal. Many HUCs ranked moderate (>20 percent mean condition) for goal 1. Several

Hydrologic unit codes ranked moderately high (>40 percent), particularly in the Cascades Range in central Washington, the Columbia River Gorge and adjacent Washington-Oregon border, the Cascade Range in central Oregon, the Klamath Basin in southern Oregon, the southern Washington-Idaho border, and a portion of the northern Great Basin in southeastern Oregon. These are areas that may warrant particular management attention.

The overall map for goal 2, maintaining long-term evolutionary potential of species, is shown in figure 63. Hydrologic unit codes with higher percentage values in this map represent locations with greater occurrence of disjunct species, and with presence of hot spots and centers of concentration of biodiversity and species rarity or endemism. As with the first goal, this map highlights areas that may warrant management attention. About half of the HUCs ranked at least moderate (>20 percent mean condition) for goal 2. Several ranked moderately high (>40 percent), particularly in the Cascade Range in southern Washington, Glacier National Park and adjacent lands in western Montana, the Idaho-Montana border, the Blue Mountains and Hell's Canyon areas of the Washington-Oregon-Idaho conjunction, and parts of the Snake River Plain and Owyhee Uplands in southern Idaho. There are likely additional HUCs that rank moderately high for goal 2 in southern Idaho for plant hot spots that did not get identified.

The overall map for goal 3, managing for multiple ecological domains and evolutionary timeframes, is shown in figure 64. Hydrologic unit codes with higher percentage values in this map represent locations with greater occurrences of unique vertebrate assemblages, and locations with large carnivores (that is, the full trophic ladder). About one-third of the HUCs ranked moderate (>20 percent mean condition) for goal 3, and none ranked high. This is not surprising, as most of the components for this goal do not overlap, by definition of unique geographic assemblages of species. Locations with moderately scored HUCs include northwestern Montana, the Greater Yellowstone

Ecosystem in western Wyoming, the Cascades Range in northcentral Washington, the Columbia River Gorge, and much of the Klamath Basin-northern Great Basin-Owyhee Uplands along southern Oregon and Idaho. Collectively, these areas cover some of the margins of the basin assessment area where unique vertebrate assemblages would be expected to be found in such a "land-locked" geography.

A cluster classification of HUCs (fig. 65) among these three images revealed that goals 1 and 2 are more similar than goal 3, as may be expected. Maintaining species viability (goal 1) suggests maintaining long-term evolutionary potential of species (goal 2). All three goals and their associated HUC maps, however, provide a full, complementary set of conditions that may prove useful for guiding ecosystem management planning at the broad scale.
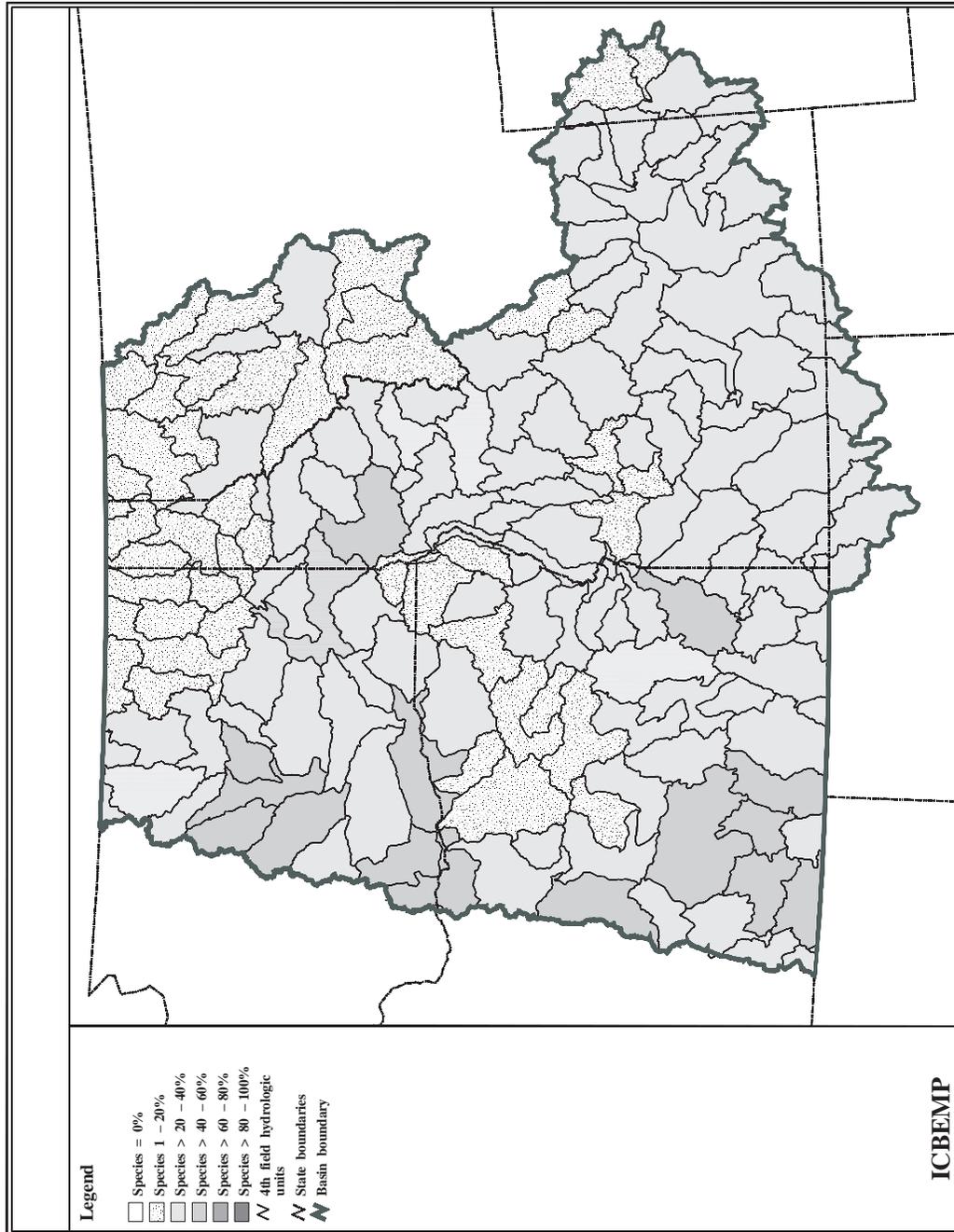
Figure 62—Composite map for ecological integrity goal 1, maintaining species viability, terrestrial components. Average percentage of all 4th-code hydrologic units in the basin assessment area among all components mapped for this goal (see figs. 44-49).

Legend

☐ Species = 0%
▨ Species 1 – 20%
▨ Species > 20 – 40%
▨ Species > 40 – 60%
▨ Species > 60 – 80%
▨ Species > 80 – 100%
∿ 4th field hydrologic units
∿ State boundaries
∿ Basin boundary

ICBEMP

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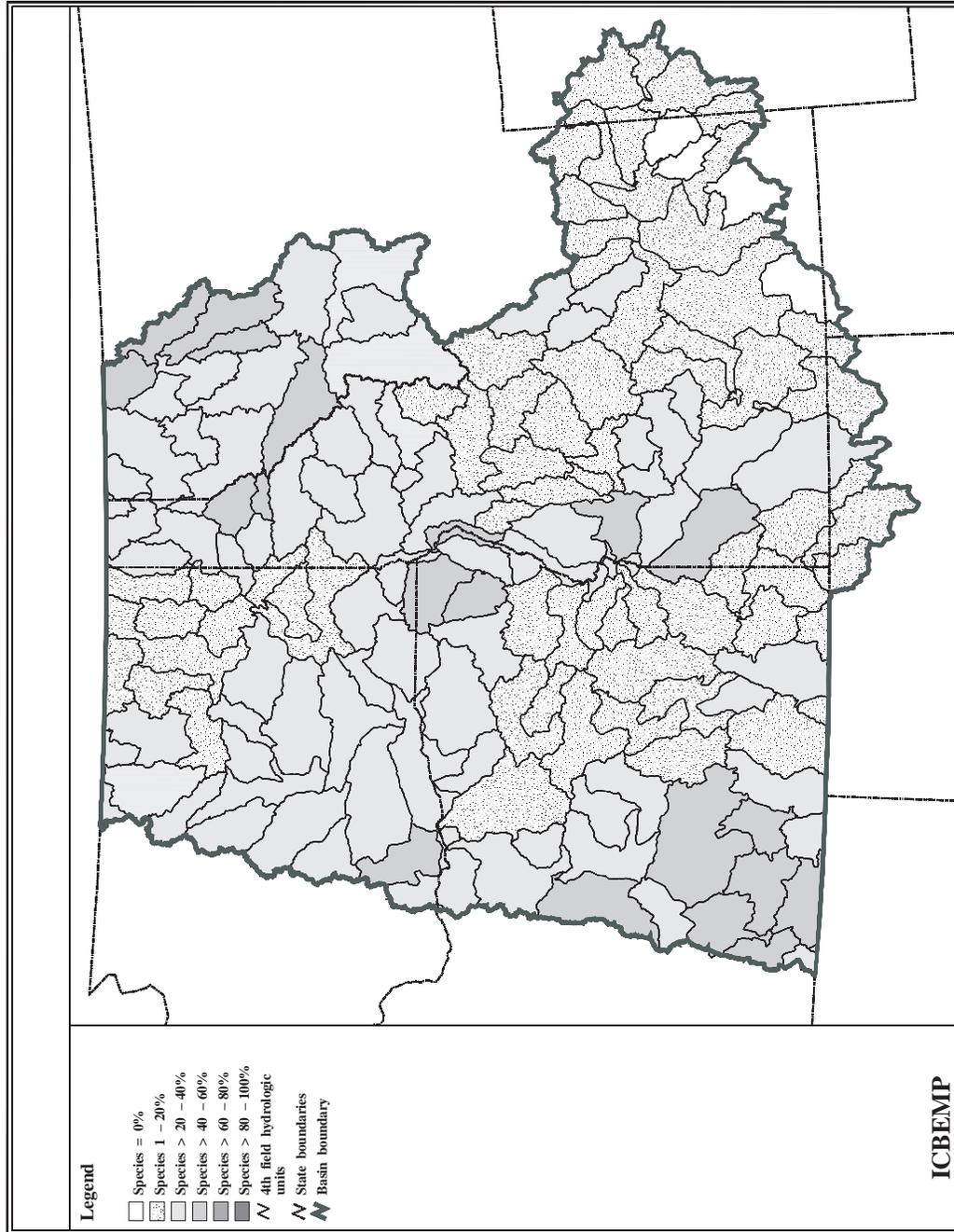
Figure 63—Composite map for ecological integrity goal 2, maintaining long-term evolutionary potential of species, terrestrial components. Average percentage of all 4th-code hydrologic units in the basin assessment area among all components mapped for this goal (see figs. 52 and 53).

Legend

Species = 0%
Species 1 – 20%
Species > 20 – 40%
Species > 40 – 60%
Species > 60 – 80%
Species > 80 – 100%
4th field hydrologic units
State boundaries
Basin boundary

ICBEMP

Legend

- ☐ Species = 0%
- ☐ Species 1 – 20%
- ☐ Species > 20 – 40%
- ☐ Species > 40 – 60%
- ☐ Species > 60 – 80%
- ☐ Species > 80 – 100%
- ∧ 4th field hydrologic units
- ∧ State boundaries
- ∧ Basin boundary

ICBEMP
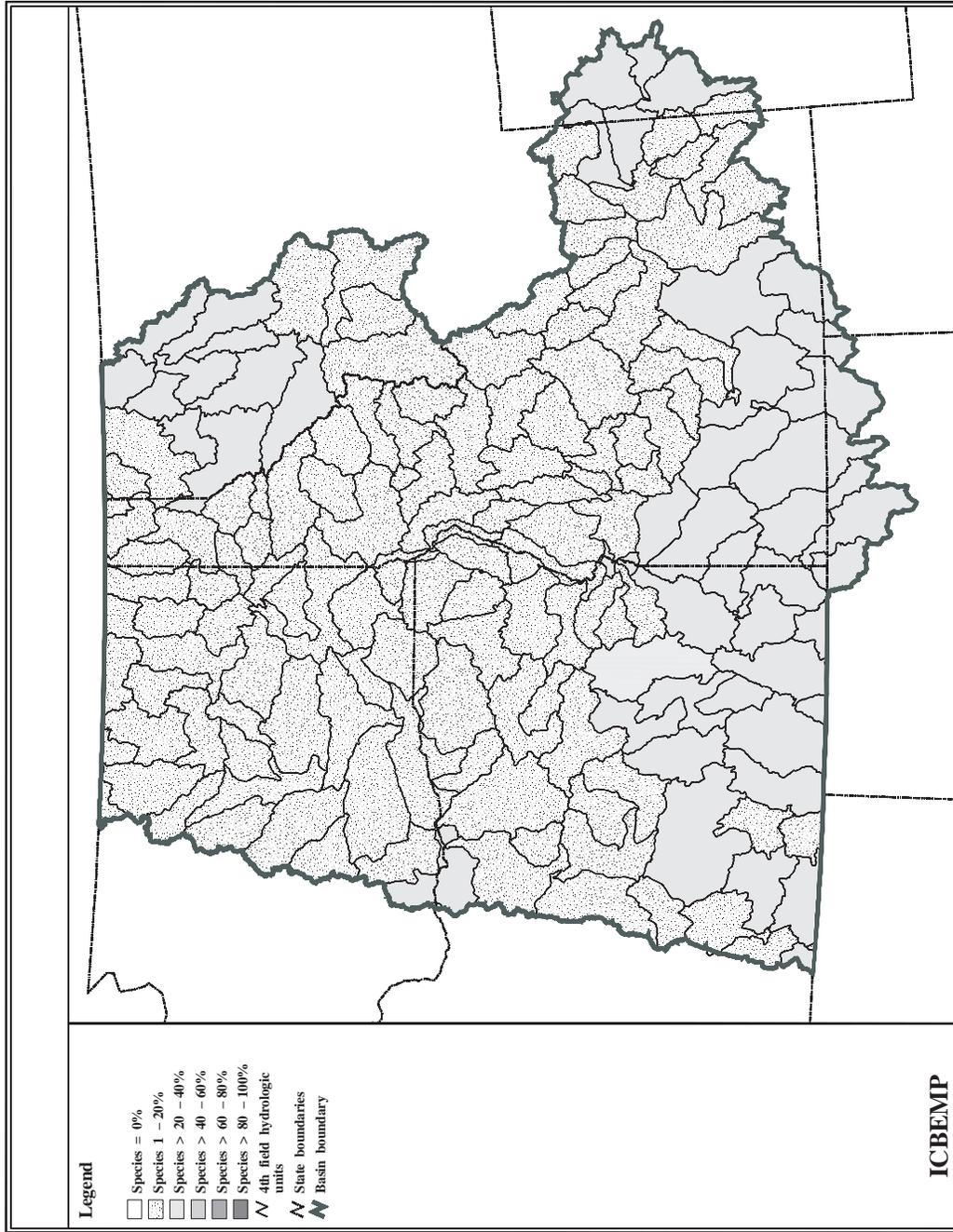
Figure 64—Composite map for ecological integrity goal 3, managing for multiple ecological domains and evolutionary timeframes, terrestrial components. Average percentage of all 4th-code hydrologic units in the basin assessment area among all components mapped for this goal (see figs. 54-61).
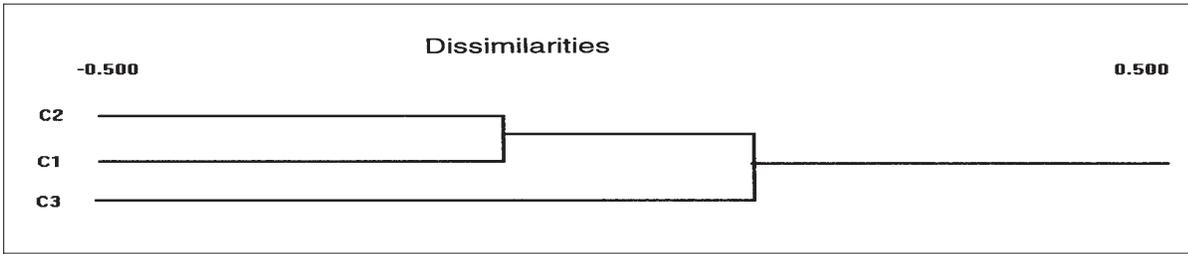
Figure 65—Cluster classification dendrogram of the three composite maps of ecological integrity goals (C1, C2, and C3; in fig. 62, 63, and 64, respectively), among 4th-code hydrologic units within the basin assessment area. Clustering was done by using complete linkage and farthest neighbor algorithms.

Chapter 5

Conclusions and Discussion

Species Functions and Ecosystem Processes

In this report, we have expanded on initial frameworks and findings (Marcot and others 1997) of KEFs of species in the basin assessment area. We tried to demonstrate basic ecological relations among species and their environments that can lead the way to greater confidence in managing ecosystems for productivity and biodiversity. We have not dealt with riparian, wetland, or aquatic systems here, particularly with their unique constellations of species' functions and ecosystem processes. But they, too, are essential parts of landscapes and need to be integrated with the terrestrial portrait.

Our treatment of species functions—as with our geographic scope—has been broad, and many facets of ecological interactions of organisms bear further telling and study. For example, Willson (1996:101) lists six categories of direct mutualisms (species mutually benefitting) of organisms in terrestrial systems, including interactions among:

- Plants and animals (pollinators, dispersal agents, woody plants and protective arthropods, and vascular plants with extrafloral nectaries and animal protectors).

- Plants and fungi (mycorrhizal associations, endophytic fungi that decrease attacks on hosts by natural enemies, and lichens).

- Plants and micro-organisms (including nitrogen-fixing microbes and angiosperms).

- Animals and other animals (plant-feeding insects and ants, interspecific flocks and herds, and other cases of animal-animal mutualisms).

- Animals and fungi (spore dispersal of mycorrhizal fungi by small mammals, wood-boring ambrosia beetles and fungal gardens).

- Animals and micro-organisms (digestive aids, surface-dwelling microbes that provide protection with pathogens).

We have discussed some examples of many of these mutualist species relations. Other commensal relations, as well as predatory, parasitic, and other kinds of ecological relations, have helped shape the composition and function of ecological communities that we observe today.

The use of species function profiles and related analyses of species' KEFs can help to (1) determine the degree of functional diversity within communities; (2) identify communities with high (or low) redundancy in specific ecological functions, and therefore communities with high (or low) resiliency or buffering capacity in the face of disturbance regimes and systematic environmental changes; and (3) identify ecological functions with high (or low) redundancy among species, in particular communities.[1] Walker (1995) suggests focusing conservation attention on functionally important species groups with little redundancy; that is, with few representative species. We may extend his suggestion to include focusing conservation attention on communities with low redundancy in (or high variation among) ecological functions. Risser (1995) notes that biodiversity can affect ecosystem functions, and suggests focusing initial management attention on the key structuring processes at intermediate scales of space and time.

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[1] All of these relations, particularly (b), need field validation.

Determining presence and redundancy of ecological functions also could be of help in posing specific goals for ecosystem restoration, particularly for augmenting natural ecosystems with restored ecosystems (Sinclair and others 1995) and by matching functional diversity in ecosystems undergoing restoration to that in undisturbed ecosystems. Examples of this include the use of species and ecosystem functions to monitor restoration progress in wetlands (Simenstad and Thom 1996) and to monitor trophic levels and feeding functions (shredders, grazers, and predators) of aquatic invertebrates in stream restoration projects (Murphy and Meehan 1991, Reeves and others 1991). Among terrestrial communities of the basin assessment area, studying patterns of ecological functions (functional redundancy and functional diversity) of forest seral stages targeted for restoration, such as old single-stratum ponderosa pine forests, could prove useful as monitoring benchmarks or to help define management targets.

Bioindicators of Terrestrial Ecosystem Health

In this report, we have further explored the potential use of lichens as bioindicators of various environmental situations, including old-growth forests, air quality, metal accumulation in soils, degree of soil acidity or alkalinity, fire and grazing regimes, and other conditions. As we discussed previously (Marcot and others 1997.), invertebrates also can serve as excellent early warning signals of existing or impending changes in environmental conditions. Sampling a small part of the invertebrate fauna, too, can help to index diversity of the entire invertebrate fauna. For example, Oliver and Beattie (1996) discovered that monitoring and assessment of terrestrial invertebrate biodiversity in Australian forests can be done by careful use of invertebrate morphospecies (species of the same morphologies)—principally ants, beetles, and spiders. Their results also suggest which invertebrate taxa to use, as well as sampling methods and sampling periods to yield the most consistent and reliable monitoring. In another study in the southern Appalachians, Hollifield and Dimmick (1995) censused arthropod availability and abundance, and they inferred from that suitability of logging roads, clearcuts, and mature hardwood forests for ruffed grouse

(*Bonasa umbellus*). Other tests of plant or invertebrate indicators are presented by Nilsson and others (1995), and Murtaugh (1996) discusses statistical analyses of indicators. Although major surveys and systematics studies are needed on invertebrates in the basin assessment area, we feel that such bioindicator approaches hold great promise for rapid field evaluations of environmental conditions and of biodiversity in this region as well.

Past and Future Changes

It is evident that the basin assessment area has undergone tremendous prehistoric change in climate, habitats, and biota. Extinctions and originations of species, genera, families, and orders have occurred over spans of millennia or longer. We expect that natural extinctions, and hope that originations (including speciations and natural immigrations of native species), will proceed long into the future. Less extreme than extinctions and originations, we also expect changes in the geographic range of species' abundance patterns over time. For example, Kruckeberg and Rabinowitz (1985) note that some rare plant taxa might become common, and some local endemics might become widespread (although not as a rule), and that the fossil record provides many instances of widely distributed taxa that have become quite constricted over time.

Patterns of evolution and extirpation of species during the Quaternary cannot be discerned from modern conditions. Conversely, recent historic persistence of species probably cannot be used to discern conditions over which species have persisted in the very long term or under which they evolved. For example, some of the climatic regimes during the early Quaternary have no modern analogs, and interglacial periods were long and extreme enough to cause extinctions but not long enough for significant plant evolution (Tausch and others 1993).

Pollen analysis from Wildcat Lake, Whitman County, Washington suggests great changes in aquatic and terrestrial environments over the past 1,000 years, with the most significant changes resulting from livestock introduction and subsequent alteration of natural vegetation, the spread of weeds, and erosion, along with volcanism (Davis and others 1977). The response of

conifer vegetation to climate change may be rapid in the more arid steppe communities of the basin assessment area. Mack and Bryant (1974) report much pine pollen in Quaternary steppe communities of the Columbia basin, thereby suggesting potentially rapid dissemination and spread of pine during periods of favorable climate.

More important and perhaps surprising, Fritts and others (1979) report that climatic fluctuations in the Columbia basin during the 17th through 19th centuries differed significantly from those during the 20th century and included large-scale variations. The range of recent historic climate does not represent that of even just the past four centuries. Therefore, use of the range of natural historic variation in suggesting prehistoric climatic conditions, and associated vegetation communities and conditions under which species persisted or evolved, may need to be greatly revised.

We know that historic changes in vegetation conditions over the last two centuries have greatly diminished habitats for some species and increased it for others. A combination of activities (principally high-grade logging, forest fire suppression, and road building) have greatly enhanced habitat conditions for many species and imperiled it for others. Lessons from this project (chapters in Quigley and Arbelbide 1997) tell us that recent land management changes and growth of human populations in the basin assessment area have been accelerating, and that we need to pay better attention to the broad-scale and long-term additive effects of local extirpations and local changes to habitats and environments.

Although global and regional climate changes from increasing concentrations of greenhouse gases in the lower atmosphere are beyond the control of BLM and FS land planning, we can nonetheless project potential outcomes and inform publics and policymakers of effects.

One point of good news is that there is no evidence that acid precipitation is a major problem for wildlife in the basin assessment area as it is in other parts of the continent. Recent studies by Vertucci and Corn (1996) suggest that high-elevation aquatic amphibians—organisms highly sensitive to and excellent indicators of acid precipitation and degradation of water quality—do not seem to be incurring this problem in the Rocky Mountains. But this does not mean that populations of native amphibians are necessarily stable; some indeed are declining for various other reasons. Beyond the assessment area, amphibian declines and disappearances have been linked to quite a list of environmental woes including chemical pollution, acid precipitation, increased ultraviolet radiation, introduction of exotic species, pathogens, harvesting by humans, and natural population fluctuations (Blaustein and others 1994), as well as increasingly dessicating climates (Pounds and Crump 1994) and depletion of atmospheric ozone (Hileman 1994). We may consider amphibians as crucial indicators of conditions to come and may use this list of environmental assailants to check our progress over time. More localized current conditions and future changes also can be heralded by heeding the health of selected lichen, plant, and invertebrate populations.

Ultimately, the productivity of habitats and their biota depends on two main factors: solar energy and soil. Solar insolation fuels photosynthesis and primary productivity, which lie at the foundation of nearly all energy pyramids and food webs. Virtually the only exceptions are the ancient Archaebacteria—a group of methanogens, halogens, and extremely thermophilic acidophiles—that stubbornly persist in high temperature and pressure environments of thermal seeps in Yellowstone, Mount St. Helens, and deep ocean vents (black smokers)[2] (Baross and Hoffman 1985). There is not much we can do about ensuring solar insolation for the rest of the terrestrial biota, except to monitor changes in climate and the atmosphere (for example, Beerling and others 1995, Dubayah 1994), perhaps by using lichens and bryophytes as litmus tests of air quality.

The soil, however, is literally at our feet and figuratively at the hand of management, and there is much we can do to monitor and guide its health. It is ironic that soil health is so influenced by microbes but manifests its effect over vast geographic areas. Its complement of macro- and micro-organisms and their vast array of ecological functions can be quickly depleted under careless management yet may take so much longer to rejuvenate. And results of site-specific management

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[2] Personal communication. 1996. P. Frenzen, Mount St. Helens National Volcanic Monument, USDA Forest Service, Washington.

activities that influence soil compaction, organic matter input, dispersal of mycorrhizae, vitality of seed banks, and persistence of microbiotic crusts, can be monitored with satellites. Maintaining ecological integrity will likely include heeding the lessons of soil by maintaining rich belowground biota with their full complement of ecological functions. In soil lies the vitality of future resources and ecosystems.

Managing for Ecological Integrity

We have identified locations within the basin assessment area that may invite attention of policy planners for meeting the three ecological goals for long-term integrity of terrestrial ecosystems at the broad scale. Terrestrial ecosystem integrity would likely benefit from further, similar assessments of our integrity components at finer resolutions for use in mid-scale planning and management activities.

Taken with assessments presented in Marcot and others (1997) and analyses in this report, we are encouraged that good opportunities still exist in the basin assessment area for meeting all three goals of terrestrial ecological integrity (that is, to maintain species viability, maintain long-term evolutionary potential of species, and manage for multiple ecological domains and evolutionary timeframes). To meet these goals, however, careful attention needs to be paid in the short term to those integrity components most at risk. These include threatened, endangered, rare, and potentially rare plants and animals; providing for species' habitats at the peripheries of their ranges and in disjunct population locations; providing for conditions to maintain hot spots and centers of concentration of plant and animal biodiversity and species rarity and endemism; and providing for habitats to maintain unique assemblages of plants and animals.

Other ecosystem integrity components of potential interest to successful ecosystem management include ensuring long-term productivity of soils and the belowground world; and attending to scarce and still-diminishing vegetation conditions, principally rare plant communities, native grasslands, native shrublands, and late seral subalpine multilayer forests. We expect, with careful salvage thinning and logging of many lower elevation forests, along with prudent reintroduction of

fire into these ecosystems, that late seral ponderosa pine single-layer forests eventually can be encouraged to return. Additional components of ecological integrity and terrestrial species conservation that may be of interest to managers in the basin assessment area are presented by Marcot and others (1997).

An Uncertain Future for Humans and Terrestrial Ecosystems: Making Tough but Informed Choices

"The extirpation of populations and species of organisms exerts its primary impact on society through the impairment of ecosystem services" (Ehrlich 1988:24). Terrestrial ecosystems continue to surprise us. Like the intricate layering of Hindu temple architecture, on closer inspection they reveal new details and structures and new services to aid human societies. For example, pharmacological and economic benefits of maintaining the full expression of plant diversity have hardly been explored in terrestrial ecosystems of the basin assessment area, but other experiences (for example, Aylward and Fendt 1995) suggest a richness yet to be realized. Likewise, we have only begun to recognize the long-term value to human societies—both native and "naturalized"—in maintaining the full diversity and productivity of terrestrial systems, principally in soils and the belowground world. Again, experiences elsewhere (for example, papers in Bissonette and Krausman 1995) shed great light on how sustainable use of natural resources can be provided by better understanding ecosystem processes and living within those means—or suffering the consequences of unnecessary resource scarcity, economic disruption, and social uncertainty (Rathore 1995).

It is not entirely clear what future effects will come of increasing human occupation of the basin assessment area, particularly from increases in roads, recreation, and human habitations in the "urban-forest interface." Although, on average, human population density of the basin assessment area is low compared with other parts of the United States (McCool and others 1997), much of the assessment area is already roaded and under active land management for various goods and services (fig. 3). Rather certain scenarios of increasing human populations (McCool and

others 1997) and rather uncertain scenarios of regional climate change together could pose grave problems and challenges to managers for maintaining a strong semblance of native biota, ecological processes, and ecosystems. Assuredly, terrestrial ecosystems of the basin assessment area will continue to exist in one form or another. But, it is not clear how *ecosystem processes* such as nutrient cycling and frequency of wildfires, *structures* such as plant and animal communities and soil microbiota, and *services* such as soil productivity, nutrient storage, and interception of surface water runoff will be altered by increasing human presence and changing Federal land management policies and activities.

Human occupation of the land often serves to sharpen boundaries between managed and unmanaged landscapes. Examples of such boundaries are rural human habitations adjacent to National Forest lands; silviculturally managed timber stands adjacent to old-growth forests or research natural areas; and grazing pastureland or agricultural fields adjacent to native *Agropyron* or *Fescue* grasslands or sagebrush steppe. Managed systems are characterized by very large fluxes in exports of soil, nutrients, pesticides, and inorganic ions, along gradients steeper than naturally occur. These changes in rates ultimately affect soils, biota, and atmospheric exchange rates (Correll 1991). In soils, pH, Eh, ionic composition, nutrient and toxic metal concentrations, and organic matter pathways can be altered (Correll 1991). Such are the kinds of complex ecosystem changes that intensive natural resource management may induce and that managers may wish to better quantify.

Our aim in this report was to contribute to understanding the history and ecology of species, communities, and ecosystems of the basin assessment area. We hope we have helped build a basis for asking the right kinds of ecological questions, and a framework for beginning to answer those questions when conducting ecosystem planning and management. We also hope that the era of terrestrial ecosystem management on Federal public lands has evolved far beyond a simple focus on threatened and endangered species and big game, although these too are legitimate and essential parts of ecosystem planning. Many ecological

relations among species affect diversity, productivity, and sustainability of ecosystems. Some relations are subject to change and can be threatened just as individual species or populations can, and thereby also warrant exquisite attention in research and management. We hope that the fruitless arguments of "species versus ecosystems" have been finally interred—as both are obviously essential and inextricable foci for understanding and for successfully managing ecosystems.

As well, an understanding of past and current situations—including variations in taxonomic groups ecological functions of species, redundancy of functions among species and communities, turnover (loss and gain) of species and taxa, and changes in climates and disturbance regimes—is fundamental to estimating the natural range of conditions, historic and present. Kay (1994) concludes that, historically, Native Americans commonly determined the structure of entire plant and animal communities by hunting and by setting fires (also see papers cited in Knowles and Knowles 1993), and that a current "natural regulation" approach to management does not recognize and thus probably would not replicate such historic conditions. He also pointed out that the historic reductions in number and distribution of beaver (*Castor canadensis*) throughout the West has had drastic effects on declining distribution of some wetland and upland ecological communities. Along with others, Kay asks the question, "What is natural?" It is a question we must answer within contexts of ecosystem policy goals, historic conditions, an understanding of prehistoric changes, background rates of extinction and origination of organisms at several taxonomic levels, the current biophysical template of the land, and even societal and political desires.

Ultimately, the range of natural conditions and ecosystem dynamics—if defined through a standard, rigorous, and repeatable process—spells out the history of the land and might provide an insight into what the land is capable of supporting in the future. Our choice as society is then to adhere to the dimensions of that envelope, or to force ecosystems into new, and usually more reduced, constitutions. At least, we hope, for terrestrial ecosystems of the basin assessment area, it will be a learned and informed decision.

Acknowledgments

English Equivalents

1 kilometer (km) = 0.62 mile

1 meter (m) = 3.281 feet

1 hectare (ha) = 2.47 acres

Degrees Celsius (^{o}C) = 5/9(^{o}F-32), where ^{o}F = degrees Fahrenheit

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Appendix 1

Categories of abundance and breeding or migration status of birds in the basin assessment area, as denoted in the species-environment relations database.

Abundance of birds:

A = Abundant
Within the right habitat and season, birds in this category would seem to be ubiquitous and numerous.

C = Common
Within the right habitat and season, birds in this category would be present.

U = Uncommon
Unlikely that birds in this category would be seen unless specifically searched for in the correct location and time. Populations are larger than those of rare birds but still not always seen when expected.

R = Rare
Seen every year but in very low numbers, usually less than 10 sightings per year. The Pacific loon, for example, is rare in Washington. Whereas the Pacific loon is out of its normal range when sighted inland, other species can be rare within their breeding range. For example, the black-backed woodpecker is a year-round resident of Montana. It breeds there but is at the edge of its range and is rarely seen because its populations are small.

I = Irregular
Usually seen in low numbers and not seen every year. An example is the Pacific loon along the Columbia River in Oregon; this species is seen in this location only in some years and always in low numbers. Another example is snowy owl, which is uncommon in the inland West when winters are harsh farther north, but which is absent in other years.

Breeding status of birds:

R = Resident
A bird species that breeds in the state and can be seen there year-round.

B = Breeding
A species that breeds in the state but winters elsewhere.

N = Nonbreeding summer resident
An unusual situation. Only a few bird species in the inland West fall into this category. One example is the blue jay, which does not breed anywhere in the inland West, but quite a few occur all summer in northwestern Wyoming.

W = Wintering
Bird species that spend the winter and breed elsewhere.

M = Migrants
Bird species present only in the spring and fall as they move between wintering and breeding areas.

Appendix 2

Lichen and bryophte species groups as bioindicators. Additional comments included here on species groups are from the Plant Task Group, SIT, Interior Columbia Basin Ecosystem Management Project (see Marcot and others 1997 for listings of specific species in each group).

Air Quality Indicators

Lichen Groups:

Bog lichens
Calcareous indicator lichens (a large group of species)
Calcareous steppe indicator lichens
Charred snag lichens (indicates recent fire)
Excess nitrogen indicator lichens
Fencepost lichens
Forage lichens
Fruticose tree lichens (only some of these species are old-growth indicators)
Leaf lichens (this is a large group of variable species)
Metal-rich indicator lichens
Moss and ditritus binders lichens
Nitrogen-fixing epiphytes lichens
Nitrogen-fixing rock lichens
Nitrogen-fixing soil lichens
Oceanic forage lichens
Oceanic leaf lichens
Oceanic log lichens
Oceanic rock lichens
Oceanic tree crust lichens
Pin lichens
Pioneer soil stabilizers lichens
Riparian lichens (indicators of high humidity)
Rock crusts lichens
Rock macro lichens (many species in this group)
Rotten log and tree base lichens (indicates ecological continuity)
Seepage lichens
Sheltered ledges and overhangs lichens
Soil lichens
Steppe soil crust lichens
Tree crusts lichens
Tundra forage lichens
Tundra rock lichens
Tundra sod builders (some species are calcareous indicators)
Urban pollution-tolerant lichens
Vagrant ground lichens

Bryophyte Groups:

Epiphytic bryophyte
Humus duff bryophyte
Peatlands bryophtye
Rock other bryophyte

Rock wet bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte

Alkaline (Carbonate) soil indicators

Lichen Groups:

Calcareous indicator lichens (large groups of species)
Calcareous steppe indicator lichens
Rock crusts lichens
Tundra sod builders (some species are calcareous indicators)
Vagrant ground lichens
Carex calcareous peatlands group (perennially saturated peat; most areas are open, but sedges on the
   edges of these peatlands are in partial shade)

Bryophyte Groups:

Aquatic submerged bryophyte
Peatlands bryophtye
Rock calcareous bryophyte
Rock wet bryophyte
Soil dry bryophyte
Soil wet bryophyte

High waterflow indicators

Lichen Groups:

Aquatic lichens (good indicators of water quality and flow levels)
Seepage lichens

Bryophyte Groups:

Aquatic submerged bryophyte
Rock wet bryophyte
Soil alkaline bryophyte

Low waterflow indicators

Lichen Groups:

Aquatic lichens (good indicators of water quality and flow levels)
Seepage lichens

Bryophyte Groups:

Aquatic submerged bryophyte
Rock wet bryophyte
Soil alkaline bryophyte

Grazing indicators-decreasers

Lichen Groups:

Calcareous steppe indicator lichens
Nitrogen-fixing soil lichens
Soil lichens
Steppe soil crust lichens

Tundra forage lichens
Tundra sod builders (some species are calcareous indicators)
Vagrant ground lichens
Carex sagebrush steppe dry group
Carex sagebrush steppe wetland riparian group (hot dry summers)

Grazing indicators-increasers

Lichen Group:

Pioneer soil stabilizers lichens

Bryophyte Groups:

Aquatic submerged bryophyte
Peatlands bryophtye
Rock wet bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte

High-nitrogen indicators

Lichen Groups:

Excess nitrogen indicator lichens
Fencepost lichens
Rock crusts lichens
Rock macrolichens (many species in this group)
Urban pollution-tolerant lichens

Bryophyte Groups:

Aquatic submerged bryophyte
Rock other bryophyte
Rock wet bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte

Metal-rich rock indicators

Lichen Groups:

Metal-rich indicator lichens
Rock crusts lichens

Bryophyte Groups:

Aquatic submerged bryophyte
Rock other bryophyte
Rock wet bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte

Old-growth forest indicators

Lichen Groups:

Calcareous steppe indicator lichens
Charred snag lichens (indicates recent fire)
Forage lichens
Fruticose tree lichens (only some of these species are old-growth indicators)
Moss and ditritus binders lichens
Nitrogen-fixing epiphytes lichens
Oceanic forage lichens
Oceanic leaf lichens
Oceanic log lichens
Oceanic tree crust lichens
Pin lichens
Riparian lichens (indicators of high humidity)
Rotten log and tree base lichens (indicates ecological continuity)
Steppe soil crust lichens
Tree crusts lichens

Bryophyte Groups:

Decayed wood bryophyte
Epiphytic bryophyte
Humus duff bryophyte
Peatlands bryophtye
Rock calcareous bryophyte
Rock other bryophyte
Rock wet bryophyte
Soil dry bryophyte
Soil wet bryophyte

High soil temperature indicators

Bryophyte Groups:

Rock calcareous bryophyte
Rock other bryophyte
Rock wet bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte
Low soil temperature indicators

Bryophyte Groups:

Peatlands bryophtye
Rock calcareous bryophyte
Rock other bryophyte
Rock wet bryophyte
Soil dry bryophyte
Soil wet bryophyte
Tundra forage lichens
Tundra sod builders (some species are calcareous indicators)
Vagrant ground lichens

Carex calcareous peatlands group (perennially saturated peat; most areas are open but sedges on the edges of these peatlands are in partial shade)

Carex noncalcareous peatlands group (perennially saturated peat; most areas are open but sedges on the edges of these peatlands are in partial shade)

Coarse soil texture indicators

Bryophyte Groups:

Peatlands bryophtye
Rock calcareous bryophyte
Rock other bryophyte
Rock wet bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte

Vascular Plant Groups:

Penstemon acuminatus group (sandy dunes and sandy areas near rivers)

Penstemon foothills to montane dry rocky group (rocky margins of old stream channels, scree, rock walls, outcrops, rocky roadcuts, and well drained areas; indicators of dry conditions)

Penstemon foothills to montane meadow group (indicators of changes in hydrologic regime)

Fine Soil Texture Indicators

Lichen Group:

Steppe soil crust lichens

Bryophyte Groups:

Peatlands bryophtye
Rock calcareous bryophyte
Soil alkaline bryophyte
Soil dry bryophyte
Soil wet bryophyte

Appendix 3

Rare or potentially rare vascular plant species as bioindicators. Note that this list includes only the rare or potentially rare species explicitly considered in this assessment. Other indicator plants that are not rare or potentially rare also can be identified. Additional comments included here on species are from the Plant Task Group, Science Integration Team, Interior Columbia Basin Ecosystem Management Project.

Alkaline (Carbonate) Soil Indicators:

Arabis fecunda
Astragalus paysonii
Botrychium ascendens
Botrychium lineare
Botrychium pedunculosum
Carex lenticularis var. *dolia*
Carex parryana ssp. *idahoa*
Chrysothamnus parryi ssp. *montanus*
Erigeron lackschewitzii
Lesquerella carinata var. *languida*
Lesquerella paysonii
Penstemon compactus
Physaria integrifolia var. *monticola*

High WaterFlow Indicators:

Artemisia ludoviciana ssp. *estesii*
Gratiola heterosepala
Grindelia howellii
Oxytropis campestris var. *columbiana*

Grazing Indicators - Decreasers (sensitive to grazing disturbances):

Astragalus sinuatus
Botrychium ascendens
Botrychium crenulatum
Carex parryana ssp. *idahoa*
Cymopterus acaulis var. *greeleyorum*
Eriogonum novonudum
Gratiola heterosepala
Lesquerella carinata var. *languida*
Lesquerella paysonii
Mimulus evanescens
Mimulus patulus
Oryzopsis contracta
Phacelia lutea var. *calva*
Phacelia lutea var. *mackenzeorum*
Silene spaldingii
Stanleya confertiflora
Thelypodium howellii ssp. *howellii*
Thelypodium howellii ssp. *spectabilis*

Metal-Rich Rock Indicators:

Haplopappus radiatus
Penstemon nikei

High Soil Temperature Indicators:

Astragalus diaphanus var. *diurnis*
Lesquerella carinata var. *languida*
Oryzopsis contracta

Low Soil Temperature Indicators:

Carex lenticularis var. *dolia*
Castilleja pilosa var. *steenensis*
Lesquerella humilis

Coarse Soil Texture Indicators:

Allium aaseae
Allium constrictum
Allium punctum
Allium robinsonii
Astragalus columbianus
Astragalus diaphanus var. *diaphanus*
Astragalus diaphanus var. *diurnis*
Astragalus mulfordiae
Astragalus pulsiferae var. *suksdorfii*
Astragalus sinuatus
Astragalus yoder-williamsii
Botrychium lunaria
Carex lenticularis var. *dolia*
Chrysothamnus parryi ssp. *montanus*
Cypripedium fasciculatum
Descurainia torulosa
Erigeron lackschewitzii
Hackelia cronquistii
Hackelia venusta
Lesquerella carinata var. *languida*
Lesquerella humilis
Lesquerella paysonii
Oxytropis campestris var. *columbiana*
Papaver pygmaeum
Penstemon glaucinus
Penstemon kingii
Penstemon lemhiensis (does well in disturbed subsoils, but seems to do best on developed, dark soils
   [mollisols] of gravelly loam texture)
Silene spaldingii
Stanleya confertiflora

Fine Soil Texture Indicators:

Aster jessicae
Astragalus sinuatus
Botrychium ascendens
Botrychium crenulatum
Botrychium lunaria
Botrychium paradoxum

Botrychium pedunculosum (successional relations unclear; species may prefer late seral grassland habitats, as well as early to mid successional forest habitat)

Calochortus longebarbatus var. *longebarbatus* (soils are colluvial)

Calochortus longebarbatus var. *peckii*

Calochortus nitidus

Camissonia pygmaea (plants at soil interface adjacent to talus)

Carex parryana ssp. *idahoa* (occurs in minerotrophic [rich] subalpine fens consisting of sedge peat; persistent, saturated emergent wetlands)

Chaenactis cusickii (ash deposits weathering to clays; few associates, almost always annuals; dry, barren sites)

Erigeron lackschewitzii (found exclusively on calcareous soil derived from dolomite; soils are cryptorthents of gravelly silt or loam)

Eriogonum novonudum

Grindelia howellii (plant occurs in many disturbed sites, but its native habitat may be upper drawdown zones of prairie ponds in the Ovando Valley)

Haplopappus liatriformis (does poorly in areas of significant grazing)

Howellia aquatilis (ponds surrounded by narrow ring of cottonwood and tall deciduous shrubs; populations fluctuate widely among years because of variation in precipitation; recent wild fluctuations of precipitation [1988-drought; 1993-wet; 1994-drought] have reduced populations)

Lepidium davisii (desert playas; hard gray-white clays; pH 6-7 at all playas; very few associated species; barren; roots deep in cracks)

Primula alcalina

Rorippa columbiae

Silene spaldingii (biscuits in biscuit-scabland on loess, alluvium, aeolian soils)

Trifolium douglasii (little known about this species)

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This report presents information on biogeography and broad-scale ecology (macroecology) of selected fungi, lichens, bryophytes, vascular plants, invertebrates, and vertebrates of the interior Columbia River basin and adjacent areas. Rare plants include many endemics associated with local conditions. Potential plant and invertebrate bioindicators are identified. Species ecological functions differ among communities and variously affect ecosystem diversity and productivity. Species of alpine and subalpine communities are identified that may be at risk from climate change. Maps of terrestrial ecological integrity are presented.

Keywords: Macroecology, paleoecology, ecological integrity, terrestrial communities, ecosystems, wildlife, fungi, lichens, bryophytes, vascular plants, invertebrates, arthropods, mollusks, amphibians, reptiles, birds, mammals, endemism, interior Columbia River basin, Klamath Basin, Great Basin.

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