



Wildlife of Westside and High Montane Forests

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Introduction

More than 300 vertebrate species are associated with western forests of Oregon and Washington (Table 1). Western and montane conifer-hardwood forests and oak woodlands are some of the more species-rich areas within the two states. Both the productivity and the mosaic of conditions within western forests contribute to the higher vertebrate diversity. These forests are exceeded in richness only by habitats encompassed by riparian-wetlands, urban, and agriculture and pasture designations. Interestingly, these are habitats that either border or are found nested within western forests. A high overlap of species occurs between these habitat types and western forests, especially along their interfaces. Forest species include those taxa that are obligates to forested habitats for all or part of their life history, more generalist species that occur in the forest matrix but also in other nonforest types, and transient species that are found incidentally in forests because of their proximity to other habitats.

This chapter provides an overview of the broad- and fine-scale patterns of western forest wildlife assemblages, emphasizing the main faunal habitat associations with forest conditions. Drivers of the geographic distributions of many taxa include climate conditions, the legacy of past natural disturbances, and vegetation types. This mix of physical and biological conditions has been elegantly consolidated into ecoregion designations for western forests. Ecoregions provide a context for broad-scale species richness pattern assessment. At finer spatial scales,

site, microhabitat, and microclimate conditions, and recent disturbance events contribute to explanations of species distribution patterns. Habitat assessments of forest-associated wildlife conducted for this volume are compiled to summarize species-habitat relations. Across spatial scales, species life history, behavior, and intra- and interspecific interactions are significant elements for our understanding of wildlife habitat associations. These abiotic and biotic components are outlined to more fully conceptualize their roles in the organization of forest faunal assemblages. Hotspots of wildlife diversity are addressed at both broad landscape and finer forest stand spatial scales.

Although all vertebrate classes have some coverage in this chapter, amphibians are used for many lead examples. Whereas amphibians do not comprise a large percentage of the overall wildlife fauna in these habitats (about 13%), western forests are key habitats for many amphibians. Of 31 native amphibian species occurring in Oregon and Washington, 29 (93%) occur in western forests (Table 1) and 22 (71%) are restricted to this region.³⁹ These restricted species are either endemic to western Oregon and Washington or have ranges within the larger ecological extent of the western forest landscape.

There are many unique amphibian taxa reliant on these forested habitats. Among these are (1) the tailed frog (Figure 1); (2) the largest terrestrially occurring salamander, the Pacific giant salamander (Figure 2); (3)

Table 1. Species occurrences (no. species) in western and montane forest habitat types of Washington and Oregon.*

Taxon	<i>n</i>	Montane mixed conifer	SW Oregon mixed conifer- hardwood	Westside oak and dry Douglas-fir & woodlands	Westside lowlands conifer-hardwood
Amphibians	29	27	19	18	26
Reptiles	20	5	19	18	14
Birds	164	107	131	119	120
Mammals	104	82	67	74	73
Total	317	221	236	229	233

* Data are compiled from expert panel assessments for this book, and no historic occurrences are included (e.g., bison, gray wolf, merlin). *n* = total no. species evaluated.



Figure 1. Tailed frogs (*Ascaphus truei*) are primitive anurans strongly associated with conditions of western Oregon and Washington old-growth forests. J. S. Applegarth, photographer.

the torrent salamanders, *Rhyacotriton* spp.; and (4) several endemic plethodontid salamanders³⁴ (Figure 3, page 197). Western forests are recognized as a region of phylogenetic radiation for amphibians, yet our understanding of the amphibian biodiversity is incomplete. As a result of ecological, morphometric, and genetic studies, formal designations of distinct populations (e.g., evolutionarily significant units [ESUs]³⁰) or species across the western forest landscape are expected to change. Within this vertebrate class, the tendency for philopatry and limited dispersal capability has resulted in isolation of subpopulations, that now seem to have diverged ecologically, morphologically, and potentially taxonomically. Support for newly recognized species, or proposals to recognize distinct populations or species, have developed for *Rhyacotriton*, *Dicamptodon*, several *Plethodon* salamanders, 2 *Rana* frogs, and 1 *Aneides* salamander. The potentially hidden biodiversity within amphibians is expected to be a topic of research for some years to come. As species are examined in this light, concern for the status of unique subpopulations or species is heightened. This has ramifications for species conservation, and consequently western forest management policies.

Final sections of this chapter address forest management and its role in maintaining the persistence of wildlife populations in the western forest region. Anthropogenic disturbances over the last 100 years have reshaped forest habitats in Oregon and Washington. A current pivot in trajectories for public land management is introducing new standards for landowner stewardship of biological resources. Consequences of both the past management policies that emphasized economic resources and the current new management directions balancing socioeconomics with ecosystem integrity are significant



Figure 2. Pacific giant salamanders are stream breeders, but after metamorphosis they are terrestrial, occurring in upslope forests. J. S. Applegarth, photographer.

for species. These have and will mold habitats, and incidentally or by design, wildlife distribution and abundance patterns. We are learning how to be stewards for the long-term economic productivity and ecological sustainability of these forested landscapes. As our knowledge gaps are filled and standards for biological conservation are adjusted, we can expect an adaptive framework for forest management policies for the next millennium.

Broad Scale Patterns

Western forests in Oregon and Washington harbor a diverse and unique fauna. From a broad regional perspective, the habitats provided by western coniferous forests across the landscape can be easily distinguished. Their high productivity and structural complexity are captured by remote sensing images (Figure 4, page 200). This is not a homogeneous landscape, however, as might seem apparent at this broad spatial scale. It is the habitat heterogeneity, both across the region and within landscapes, that is pivotal to understanding the wildlife diversity of the western forests.

The large-scale mosaic of habitats across westside and montane forests is exemplified by the multiple physiographic provinces or ecoregions for this area. Physiographic province designations take primarily physical factors into consideration, including soils, geomorphology, natural disturbance history, and climate. When discussed in light of wildlife distributions, Nussbaum et al.³⁷ recognized 3 physiographic provinces over the western forest landscape (Cascade Mountains, Coast Ranges, and Klamath Mountains). These are subdivided into 8 physiographic provinces in the Recovery Plan for the northern spotted owl⁵⁶ (Cascade Mountains into 4 provinces: eastern and western Cascade Ranges in

both Oregon and Washington; Coast Ranges into 3 provinces: Olympic Peninsula, Washington lowlands, Oregon Coast Range; and the Klamath Mountains). Ecoregions are geographic descriptors of environmental conditions; they are based on spatial patterns of physiography, climate, disturbance, vegetation, and wildlife. Omernik⁴⁰ recognized 5 Level III ecoregions for the area of interest in this chapter (Coast Range, Cascades, Eastern Cascades and foothills, North Cascades, Klamath Mountains); these are analogous to some of the physiographic provinces above. Pater et al.⁴² provided a further subdivision of the Level II ecoregions into 42 Level IV regions (Figure 5, page 198).

Whereas general wildlife patterns were criteria for ecoregion determination, correspondence of wildlife species distributions with ecoregions is not fully investigated. Evaluation of species' associations with the newly developed Level IV ecoregions for western Oregon and Washington have not been conducted. However, some initial pattern assessments have developed using Oregon Level III ecoregions. The Oregon Biodiversity Project⁴¹ presented species richness categories on a hexagonal grid for the State, with 150,000-acre (60,750-ha) hexagons, for butterflies, amphibians, fish, reptiles, and mammals (Figure 6, page 201).

Across Oregon, fish species richness was greatest in the western portion of the state coincident with western forests (many hexagons with >20 species and >29 species), compared to east-side areas (<8 species in much of the southeastern portion of the state, and patches from <8 to 20-29 species in the northeastern portion). In the Cascades, fish species richness decreased with increasing elevation. Mammal and butterfly richness patterns were similar to each other, although mammals were less variable in richness numbers across the western forested landscape. These 2 taxa had greatest diversity in the southern Cascade Range and up the ridge of the Cascade crest (including portions of the Klamath, and eastern and western Cascade ecoregions; >102 butterfly and >64 mammal species in much of this area). In contrast, among the western forested regions, butterfly and mammal richness were least in the Coast Range. Amphibian patterns in this analysis were extremely patchy. Like fish, diversity was greater in the western forests, with the least richness in the eastern Cascades. Among the other 3 western forested ecoregions, each had some hexagons with higher amphibian diversity (>15 species), most with intermediate (7-15 species) richness categories, and a number of patches with <5 amphibians. Reptile richness showed the most remarkable concordance with ecoregion boundaries. Among western forested regions, reptile richness was highest (>15 species) in the Klamath region. Much of the Coast Range had the lowest reptile richness category (<6 species), and the western Cascades showed a decreasing richness with elevation, with 12-15 species in the foothills and 6-8 species in the higher landscape.

Although Oregon bird species richness patterns were not compiled for the Oregon Biodiversity Project,⁴¹ bird species ranges correspond to several patterns related to

western forest ecoregions. Nine general species range patterns were derived from avian range maps in Csuti et al.¹⁶ (Figure 7, >240 species evaluated, shorebirds restricted to coastal shores were excluded). Proportion of species per pattern and example species are (1) 2%, northern spotted owl and harlequin duck; (2) 8%, MacGillivray's warbler and varied thrush; (3) 3%, purple finch and chestnut backed chickadee; (4) 22%, American dipper and dark-eyed junco; (5) 2%, plain titmouse and black phoebe; (6) 7%, boreal owl and three-toed woodpecker; (7) 6%, calliope hummingbird and flammulated owl; (8) 9%, northern flicker and common raven; and (9) 39%, western meadowlark and yellow-headed blackbird. Half of the bird species in Oregon and Washington have the majority of their ranges in westside forests (patterns 1-7, Figure 7.) Most western forest birds have some occurrences east of the Cascade Range (e.g., patterns 2, 4, 5, and 7), and relatively few have ranges restricted to westside forests (e.g., patterns 1, 3, and 6).

Such a species range assessment provides a slightly shifted perspective of the spatial arrangements of species in comparison to species richness maps (e.g., Figure 6). For comparison among wildlife vertebrate taxa and between Oregon and Washington, additional range patterns were assessed (Figure 8). To facilitate comparisons, patterns 1 through 4 were combined to consolidate species with general west-side forest relationships, and patterns 6 and 7 were combined to more easily represent species restricted to the Cascade Range. In Oregon, forests in the Cascade Range and westward (Figures 7 and 8, general range patterns 1 through 7) are focal portions of the ranges of >50% of the species in each of these vertebrate classes. However, for all vertebrate classes assessed, east-side landscapes provide significant habitats for some species (Figures 7 and 8, general range pattern 9). This fact might be overlooked if only species richness maps were examined. For example, amphibian species richness (Figure 6) is clearly tied to western forests, yet east-side landscapes are of critical importance for the ranges of about 20% of Oregon and Washington amphibian species (Figure 8, general range pattern 9). Interestingly, reptiles in Washington are much more reliant on east-side habitats than those in Oregon (Figure 8). In Oregon, the west-side Klamath ecoregion contributes a significant reptile species "hotspot."

Herpetological distribution patterns in the Klamath ecoregion are further addressed by Bury and Pearl.⁴ They reported that this region has the most species-rich herpetofauna of any similar-sized mountain range in the Pacific Northwest (38 native species of amphibians and reptiles; this number reflects total richness for the region, as opposed to richness per hexagon in the previous discussion). As already noted, this is largely attributable to the higher reptile richness in the Klamath region. Bury and Pearl⁴ provided explanation for this patterning based on organism ecology, life history and behavior, and the common data elements that go into defining ecoregions (e.g., elevation, latitude, climate, legacy of past natural disturbance events, vegetative structure and composition).

Figure 7. General range patterns of Oregon birds, derived from species range maps in Csuti et al.¹⁶ Dark shading indicates the main portion of species ranges (areas in which most localities or habitats are known), light stippling indicates some occurrences, white indicates no or very few localities are known. Level III ecoregion boundaries (Figure 5) are used for general range boundaries.

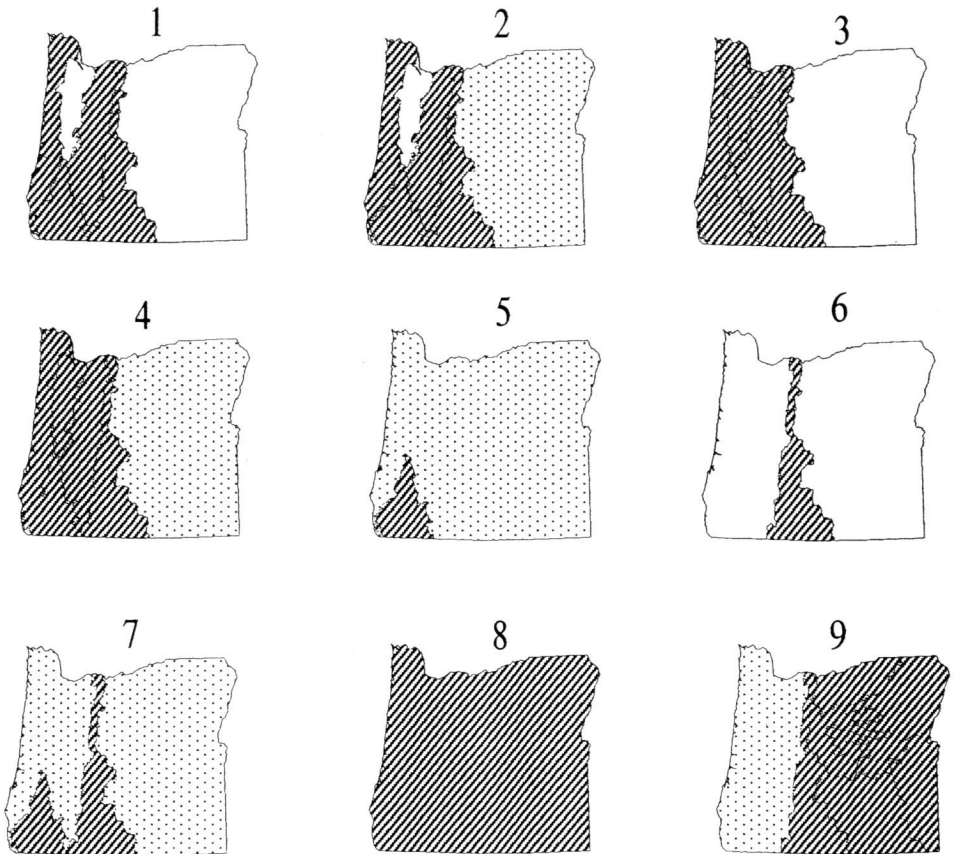
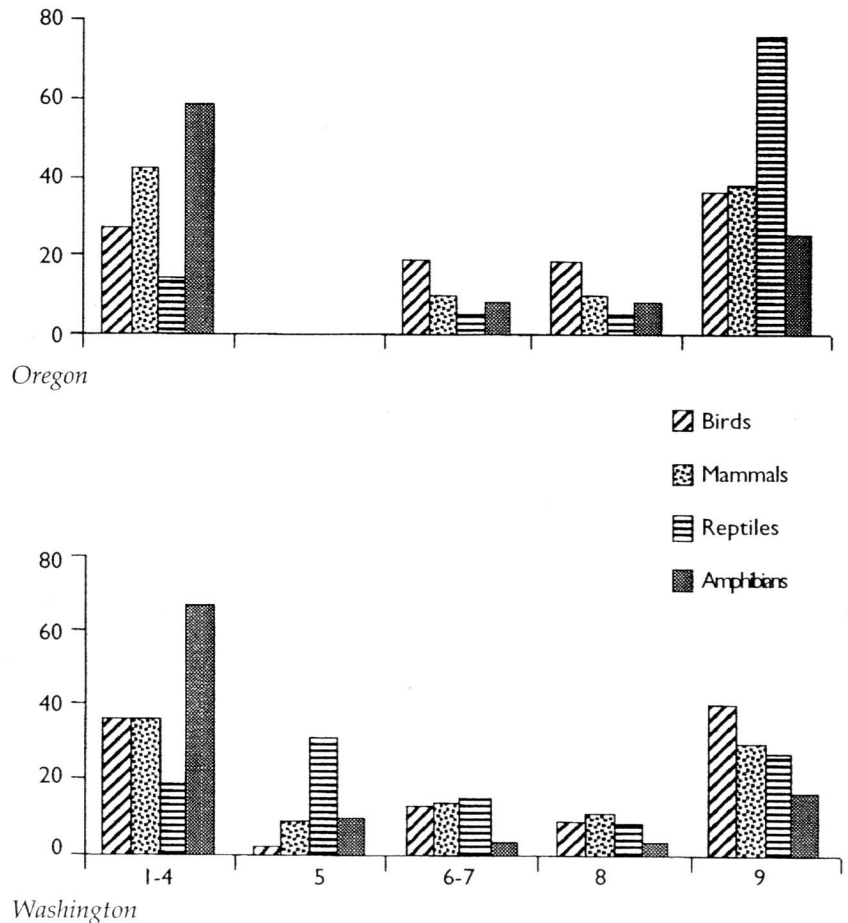


Figure 8. General range patterns (1-9 from Figure 7) of Oregon wildlife and extension of those geographic patterns in Washington. Patterns 1-4 from Fig. 7 are combined to represent taxa with predominantly west-side ranges, and patterns 6 and 7 are combined to represent species occurring primarily in the Cascade Range. Data are compiled from range maps in Csuti et al.,¹⁶ Johnson and Cassidy,²² Leonard et al.,²⁵ Smith et al.,⁴⁶ and Storm and Leonard.⁴⁸



These are the puzzle pieces that must be evaluated to understand the broad-scale species richness trends for any wildlife taxa. This rationale for herpetofauna of the Klamath ecoregion can be extended to demonstrate probable drivers of regional patterns in the western forests of Oregon and Washington.

Across western Oregon and Washington forests, many wildlife species diversity patterns are established with latitude, elevation, and climate, some of the basic data elements of ecoregions. These factors interact to produce different biotic and abiotic environments for wildlife, and species composition changes markedly with these factors. Taxa reliant on temperature and moisture regimes, such as reptiles and amphibians, show strong physiographic associations.³⁷ For example, species richness decreases with increases in latitude and elevation for reptiles and amphibians in western forests as temperature and moisture tolerance limits are encountered. Among amphibians occurring in the Cascade Range, approximately 20 species generally occur at elevations <4,000 ft (1,219 m), 13 species at 4,000-5,000 ft (1,219-1,524 m), 9 species at 5,000-6,000 ft (1,524-1,829 m), and 7 species at >6,000 ft (1,829 m, range limits compiled from Leonard et al.²⁵). Latitudinally, reptile species distributions become much more restricted to the north: only 3 of about 18 species retain broad distributions, 8 species are found primarily within the inland valleys (e.g., Willamette Valley), and 7 species' ranges end with the Klamath Mountains ecoregion. In southern Oregon, amphibian species gradients are found with distance from the coast. Presumably the cooler, moister climates of the coastal zone may explain this; conditions become xeric rapidly inland. Of 9 salamanders occurring at the coast in the extreme southwestern corner of the state, only 5 have likely ranges extending through Jackson County, about 100 miles (161 km) inland (Pacific giant salamanders, roughskin newts, *Ensatina*, clouded salamanders, and Del Norte salamanders are "replaced" by Siskiyou Mountain salamanders; Figure 3).

Current broad distributions of many taxa also reflect a legacy effect of past natural disturbances or environmental conditions. In particular, less vagile taxa with specific habitat requirements are not as resilient to disturbances, and their distributions may retain a signature of past events for extended time periods. The development of the Pacific Northwest herpetofauna and current herpetofaunal distributions were summarized by Nussbaum et al.³⁷ in light of the regional-to-continental extent of the northern temperate rain forests comprising the Arcto-Cretaceous-Tertiary Geoflora, and subsequent orogenic, glaciation, and drought events. They surmised that some currently depauperate areas can be accounted for by both insufficient time for reinvasion and the current relatively cold, harsh environments restricting colonization. They proposed that reptiles with broader distributions elsewhere and peripherally distributed in the Pacific Northwest may be relatively recently introduced to this region subsequent to the last glaciation (25,000-10,000 years ago). Many of the region's reptiles are derived from

species in the southwestern U.S., which presumably moved north with the retreating glaciers and establishment of warmer, more xeric conditions.

Likewise, amphibians responded to the same combination of events, the broad-ranging temperate forests subject to subsequent mountain-building, glaciation, and drought. Yet rather than these events resulting in colonization from adjoining regions, as in reptiles, many amphibian populations became isolated as the temperate rain forests contracted from their historical extent, becoming fragmented, with inhospitable conditions developing between remnants. Both glaciation and drought exacerbated isolation of such species dependent on milder conditions. Welsh⁵¹ elaborated on this scenario in his presentation of relictual amphibian species adapted to the ancient primeval coniferous forest ecosystem. Several species now associated with old-growth forest conditions may be relics of this historical forest landscape, now strongly tied to stands retaining a semblance of the microhabitat and microclimate conditions of yore. Welsh's⁵⁹ analyses from southwestern Oregon and northwestern California identified the Del Norte salamander, the tailed frog, and the southern torrent salamander as such relics that generally do not tolerate conditions in highly managed forest stands. As presented by Welsh,⁵⁹ relatively small sedentary organisms with restricted distributions and narrow habitat requirements and climatic tolerances would be sensitive to disturbance or environmental change. Many of the 22 native amphibian species restricted to the western forest landscape occur in association with old-growth forest conditions, and are in essence phylogenetically symbolic of a past legacy of events and conditions in this region. Isolation scenarios based on disturbance and changing environments can be conceived for many of them (e.g., the plethodontids in Figure 3). The current distribution of the Larch Mountain salamander (Figure 3) likely reflects volcanic disturbance events from Mount Saint Helens, Mount Rainier, and Mount Hood, in addition to spatio-temporal fluctuations in microhabitat and microclimate conditions. Such dot map distributions also reflect biases of survey locations (i.e., remote areas are less sampled).³⁴

Synthesizing the data contributing to ecoregion designations can lead to a better understanding of "hotspots" of wildlife diversity at the broad spatial scale of western and montane forests. As discussed, reptile diversity is highest in the more xeric Klamath Mountain region. The margins of several species ranges occur here, at their northern or western extent, whereas those that are found to the north often show more restricted distributions to lowland areas. Birds mirror this pattern (see Case History 1, below). DellaSala et al.¹⁷ referred to the Klamath-Siskiyou ecoregion as an area of "extraordinary biodiversity", ranking its biodiversity "among the world's most outstanding temperate coniferous forests". Of 2,377 terrestrial animals they analyzed (snails, butterflies, birds, mammals, reptiles and amphibians), 168 (7%) occurred nowhere else. They found high endemism among aquatic animals: 42% of fish ($n=33$),

and 60% of mollusks ($n=235$). At the subspecies level, 281 (8%) of >3,500 plants were cited as endemic. A dominant contributor to the Klamath-Siskiyou wildlife diversity hotspot is the convergence of several mountain ranges, in an "H" pattern. As a result, there is juxtaposition of several highly dissected stream drainage networks, extensive elevational and microclimatic gradients, and relative proximity of different life zones or ecoregions: the high desert of the Great Basin (east); California mountains (i.e., Sierra Nevada), plains and valleys (south); Coast (west); and the inland wet-temperate river valley systems (in the Klamath region and north to the Willamette Valley). In addition to the diverse array of physical conditions and vegetation types from the intersection of these zones, the survival of relictual flora and fauna due to reduced glacial impacts and, consequently, remnant habitats in this area adds a legacy effect to its biological diversity. For amphibians, at a provincial or ecoregion level, a broader ranging diversity hotspot occurs in the more productive wet temperate forests of the Coast Range.³⁷ Broad-scale diversity hotspots for mammals are less easily identified. Diversity hotspots may be distinguished at finer spatial scales, and are discussed below relative to patterns resulting from more fine-grained habitat elements.

Case History I

Patterns of Bird Communities in Coniferous Forests of Western Oregon and Washington

Joan C. Hagar

The majority of bird species occurring in conifer-dominated forests west of the Cascade crest in Oregon and Washington are widely distributed within this zone. Chestnut-backed chickadees and varied thrushes are notable residents of moist, low elevation (<5,000 ft [1,524 m]) coniferous forests west of the Cascade crest because they are broadly endemic to the Pacific Northwest and coastal southern California. Other year-round resident species that are characteristic of these forests include northern spotted owl, pileated woodpecker, Steller's jay, winter wren, and golden-crowned kinglet. During the breeding season, migrant species swell the ranks of the avifauna in terms of both numbers of species and density of individuals. Among the most broadly distributed and abundant migrant species in these conifer forests are the Swainson's thrush, Pacific-slope flycatcher, and hermit warbler. The breeding distribution of hermit warblers is largely restricted to Washington, Oregon, and California, defining this species as an endemic.

Avian community composition is influenced by elevation, seral stage, vegetation structure and composition, presence of water and other special features, and the interaction of all these factors. Total bird abundance in western Oregon and Washington is generally negatively correlated with elevation.²¹ A negative relationship between elevation and bird species richness in old-growth forests also has been reported.²⁴

Changes in riparian bird communities along an elevational gradient contribute to the decline in species richness with increasing elevation. Several riparian obligate species, such as great blue heron, wood duck, osprey, and kingfisher, are most abundant at low elevations, where forests or trees adjacent to large streams, rivers, and estuaries provide habitat for nesting, roosting, and foraging. At higher elevations, fewer species are strongly associated with steep, highly constrained streams and riparian vegetation that typically is only subtly distinguished from surrounding upslope forest. Dippers, however, specialize in foraging and nesting along such clear, swift mountain streams throughout western Oregon and Washington.

Bird community composition varies with seral stage, with differences being most pronounced between very early open canopy (i.e., grass-forb-shrub) and closed canopy stages. Species richness of birds tends to be similar in early and late stages of forest development, and lowest in the structurally simple mid-seral stages of managed forests.² Although relations between abundance and seral stage vary for many species on a geographic scale,⁴⁴ species that are typically associated with early seral conditions west of the Cascade Range include willow flycatchers, white-crowned sparrows, song sparrows, and spotted towhees.^{2, 11, 57} Species that typically are more abundant in old forests include Pacific-slope flycatcher, varied thrush, and many members of the bark-foraging guild (e.g., brown creeper, chestnut-backed chickadee, red-breasted nuthatch, hairy woodpecker⁴⁴). The avian species that are most closely associated with old-growth forests are marbled murrelets, northern spotted owls, and Vaux's swifts.⁴⁴ However, most species that reach their greatest abundance in older forests nonetheless also will use early seral habitats as long as key structural features are present. For example, species that forage on bark and nest in cavities, such as chestnut-backed chickadees and red-breasted nuthatches, occur in recent harvest units where green trees and snags have been retained.^{11, 57}

Hardwood trees and shrubs may be one of the most important factors influencing bird community composition in the conifer-dominated landscape of the Pacific Northwest. The abundance and diversity of birds has been correlated positively with the abundance and distribution of hardwoods.^{7, 19, 20, 21, 26, 32, 43} Deciduous hardwoods provide different resources for foraging and nesting than conifers, and thus provide unique habitat with which several bird species are strongly associated. Warbling vireos are predictably found in alder groves, and several species of neotropical migrant warblers (e.g., MacGillivray's, orange-crowned, Wilson's) typically forage and nest in thickets of deciduous shrubs.^{16, 31} Unique associations between individual avian species and either hardwoods or conifers result in high bird diversity where hardwoods are mixed with or adjacent to conifers. Examples include the margins of large valleys where Oregon white oak occurs and the Klamath region.

Provincial Bird Patterns

Few bird species have a close affinity to only one physiographic province or ecoregion, but species richness and abundances of many species vary among provinces. Although direct comparisons of avian species richness across all provinces are not available, some general patterns are evident. Total bird abundance in western Oregon and Washington is generally correlated negatively with latitude and positively with longitude.²¹ Thus, mean abundance and species richness of diurnal breeding birds is higher in the Oregon Coast Range than the Cascades of Oregon and southern Washington,²¹ and species richness is highest in the Klamath region. Characteristics of the avifauna that distinguish each province are described below.

The avifauna of the tall, dense forests of the Coast Range and Puget lowlands shows some influence of the proximity to ocean, bays, and estuaries. The marbled murrelet is a unique example of this coastal influence, being the only seabird that nests in forest habitats. Limited by the necessity to feed at sea, this species nests only within 60 miles of the ocean, and predominantly in old-growth forests where branches of sufficient diameter provide nest platforms. No bird species is particularly associated with the coastal band of Sitka spruce, but wrentits are notable for the area because they do not regularly occur west of the coastal scrub along the southern and central Oregon coast.

As in the Coast Range, dense coniferous forests dominate habitats of the lower west slopes of the Cascade Range, so it is not surprising that the avifaunas of these two ecoregions are very similar. In Oregon, a slightly lower average avian species richness on the lower west slopes of the Cascades²¹ may be partially attributable to a lower abundance of broad-leaved deciduous trees, such as big-leaf maple and red alder, than in the Coast Ranges.³⁵ On the other hand, some habitats that are unique to the Cascades contribute some distinctive members to the bird community. For example, two duck species, bufflehead and Barrow's goldeneye, breed on lakes in the high Cascades, and are considered forest associates because they use cavities, usually in snags, for nesting. Harlequin ducks are associated with fast-moving mountain streams, and find ideal breeding habitat along drainages of the west slope of the Cascades. Breeding populations of these three duck species are patchy and local throughout the Cascade Range in Oregon and Washington. Other species that are more likely to occur in the Cascades than in other provinces include golden eagle and goshawk.

Changes in bird communities that can be attributed to elevation are more obvious in the Cascades and Olympics than in the Coast Ranges. For example, Clark's nutcrackers do not occur below the high elevation spruce-fir forests in the Cascades, and mountain chickadees replace chestnut-backed chickadees above the Douglas-fir zone.¹⁶ The presence of species such as great gray owls, boreal owls, black-backed woodpeckers, and boreal chickadees in the high Cascades (>5,000 ft [1,524 m]), North Cascades, and high Olympics indicates the boreal influence on these

communities. In addition, merlins, northwestern crows, black swifts, and pine grosbeaks distinguish the avifauna of the north Cascades in Washington from those south of the Columbia River. Although both hermit warblers and Townsend's warblers breed in both states, hermit warblers reach the northern extent of their contiguous range in Washington, and Townsend's warblers do not breed south of northern California. Thus, Townsend's warblers are more abundant in the Washington Cascades, while hermit warblers are prevalent in Oregon, and the entire region comprises a zone of hybridization for these two species.

The Klamath region in southern Oregon stands out from the rest of the Pacific Northwest for two reasons: high plant species diversity, and the convergence of several ecological zones and their associated fauna. The highest avian species richness west of the Cascade crest in Oregon and Washington occurs in the Klamath Mountains. The high diversity of birds in this region has been attributed to the diversity of vegetation, and in particular the abundance of hardwoods.⁴³ Several avifaunas converge in the Siskiyou-Klamath mountains. Species such as Allen's hummingbird, black phoebe, oak titmouse, and blue-gray gnatcatcher reach the northwestern extent of their geographic ranges in this region. Species that are typical of pine habitats to the south and east (e.g., Lewis' woodpecker, white-headed woodpecker), and of Great Basin habitats (e.g., calliope hummingbird, green-tailed towhee, ash-throated flycatcher) occur in forested areas within this region. Other representatives of southern or arid regions are more abundant here than further north (e.g., acorn woodpecker), but the full compliment of species that are characteristic of moist coastal forests also occur (e.g., varied thrush, marbled murrelet, hermit warbler).

Patterns within Landscapes

Narrowing our focus from the broad regional scale perspective of species distribution patterns to a finer within-landscape approach (i.e., within the five Level III western forest ecoregions) allows a more concise discussion of wildlife-habitat relations. Whereas coarse-grained elements such as legacy disturbance effects and regional climate gradients may help our understanding of regional taxonomic diversity trends, individuals of a species survive and reproduce at finer scales. In the western and montane forests of Oregon and Washington, micro- to macrohabitat conditions at the forest stand level are of critical importance to the individual. Aggregating up in biological organization, populations similarly function within these narrower bounds. In this section, the dominant finer scale habitat associations of western forest wildlife within landscapes are presented, including forest plant species and stand structural conditions. Key habitat elements within western forests to which wildlife have strong ties (e.g., logs, rock substrates, litter, snags, and large trees) are distinguished. Old growth, young seral stages, riparian forests, and forest edges are highlighted because of their roles as wildlife habitat hotspots for

various taxa within our current managed landscapes. At this finer spatial scale, heterogeneity among these habitat types and microhabitat features remains a dominant driver of the western wildlife species diversity.

Current knowledge of wildlife species' use of habitats and general ecology in Oregon and Washington was compiled by panels of species-experts and is presented in several matrixes on the CD-ROM accompanying this book. This expert knowledge includes data supported by research, personal observations, or expert opinion. In the tables below, these data are summarized to show wildlife relationships with forest habitat type, structural conditions, habitat elements, and trophic and organismal relations.

Forest Habitat Types and Structural Conditions

Western forests are a complex mix of vegetative conditions. Herb, shrub, and canopy tree structure and composition are key predictors of the occurrence of various wildlife species. Wildlife species were assessed relative to 4 western forest habitat types: (1) Westside Lowlands Conifer-deciduous Forest; (2) Westside Oak and Dry Douglas-fir Forest and Woodlands; (3) Southwest Mixed Conifer-Hardwood Forest; and (4) Montane Mixed Conifer Forest. Fairly similar numbers of total species occurred in these habitats (Table 1), with differences reflecting some of the larger scale patterns already discussed (e.g., reptiles).

Table 2. Western forest wildlife habitat associations with vegetation height and successional stage.¹

Taxon	Grass/forb	Shrub/seedling	Sapling/pole	Small trees	Medium trees	Large & giant trees
Amphibians ²	19	19	20	21	28	28
Reptiles ³	19	16	16	18	18	17
Birds ³	61	92	98	130	140	140
Mammals ³	66	65	64	72	79	78
Total	165	192	198	241	265	263

¹Data are compiled from expert panel assessments for this book, see accompanying CD-ROM. Numbers of species are indicated.

²These species require specific habitat elements to occur within these structural conditions.

³These species may require specific habitat elements to occur within these structural conditions.

Table 3. Numbers of western forest wildlife species associated with tree size (large includes giant trees) and canopy complexity (single = single story canopies, multi = multiple story canopies).*

Taxon	Small trees		Medium trees		Large trees	
	single	multi	single	multi	single	multi
<i>Amphibians</i>						
Open	21	21	22	22	24	22
Moderate	21	21	22	28	24	28
Closed	20	21	22	28	28	28
<i>Reptiles</i>						
Open	17	18	16	15	17	16
Moderate	10	9	10	9	10	9
Closed	6	6	6	6	6	8
<i>Birds</i>						
Open	106	96	115	104	121	114
Moderate	89	85	97	101	102	104
Closed	68	67	74	76	76	96
<i>Mammals</i>						
Open	61	62	68	58	71	73
Moderate	54	54	65	60	69	68
Closed	33	41	43	47	53	65

* Data are compiled from expert panel assessments for this book.

Table 4. Numbers of species using (use) and closely associated (close assoc.) with old-growth forests in western Oregon and Washington, and their relative dispersal ability (stand is within approximately 60 acres [24 ha]; range = across provinces).¹

Taxon	Use	Close assoc.	Close assoc. in Oregon	Close assoc. in Washington	Dispersal of close assoc.
Amphibians	31 ²	16	16	10	Stand
Reptiles	10	0	—	—	—
Birds	119	38	38	37	Stand to Range
Mammals	67	26	21	21	Stand to Range
Total	227	80	75	68	

¹Data compiled from Thomas et al.,⁵¹ and includes species from northwestern California forests.

²The former Olympic salamander is represented here as the 4 torrent salamander species.

Within these 4 habitats, forest/woodland structural conditions were identified. Three components were used to classify structure: vegetation height and successional stage (i.e., grass/forb, shrub/seedling, sapling/pole, and small-to-giant tree categories); number of canopy layers (single or multiple); and canopy cover (open, moderate, closed). Several patterns of wildlife associations with these components are apparent (Tables 2 and 3). Total species richness increases with vegetation height, and this holds true for each taxon except reptiles (Table 2). Bird species show a particularly dramatic response to vegetation height, successional stage, and canopy layers. Mammals and amphibians show a similar but dampened pattern. All 4 wildlife groups show a pattern with canopy closure (Table 3). Greater numbers of birds, mammals and reptiles are associated with open rather than closed canopies. The reverse is apparent for amphibians.

Associations of western forest fauna with forest age-size or successional stage categories have been analyzed in numerous studies and assessments across the region. Results from these studies and existing knowledge of species' forest associations were compiled for the Report of the Scientific Analysis Team⁵¹ for areas within the range of the northern spotted owl. The particular assignment for this assessment was to identify those species likely to be closely associated with late-successional and old-growth forest conditions, from the longer list of those that used forest habitats (Table 4). Close associates met one of several criteria, such as having greater abundance in old-growth forest than in mature or pole stands and requiring habitat components that are contributed by old-growth forest (Table 5-1 in Thomas et al.⁵¹). From their data compilation, about a third of the vertebrates using western forests were identified as likely close associates with the older forest conditions (Table 4). No reptiles and about half the amphibians were close associates. These patterns may be reflected in the current habitat assessments. About a third more forest wildlife species occurred in association with large trees than the earliest successional stages. However, there was only about a 10% increase between small and large trees (Table 2). Amphibians were more associated with closed canopies. Structural conditions of old-growth forests include components in Table 3 that are

related to vertical stratification: large tree size, multiple story, and closed canopies. These create habitats or conditions to which some old-growth associates are reliant (see Habitat Elements below).

Some old-growth associated species do not spend their entire life in these forests. For example, neotropical migrant birds spend their winters in Mexico or Central America (7 species), and some waterfowl migrate in winter to lowland bays, lakes, and surf zones (6 species). Similarly, many aquatic-breeding amphibians reproduce in lentic and lotic waters within the forested landscape, and move to the upslope forest matrix after metamorphosis from their aquatic stages.

Early successional stands are used by many western forest-dependent wildlife. From Table 2, herb, shrub and sapling conditions are used by a high percentage of species in every taxonomic group. Open conditions across tree size categories are especially important for birds and mammals (Table 3). Similarly, 13 (25%) of 53 mammal species were associated with early seral stages in the Augusta Creek watershed, in the western Oregon Cascade Range.¹⁸ McGarigal and McComb²⁷ reported about a third of bird species ($n=99$) used early seral forests in western Oregon.

Riparian forests are critical to the life history of numerous vertebrates in western Oregon and Washington. The western forest landscape in the Pacific Northwest is highly dissected by stream channels, and the stream-upslope interface is not far from any locale in the forest matrix. Riparian areas are distinguished by their cool, moist environments, and by their multitude of conditions across a watershed. Small headwater streams are ecologically distinct from their downstream mainstem counterparts. Along this entire aquatic network, riparian areas are prone to small-scale disturbances, such as flooding, bank and slope slippage, landslides, and treefalls. These add heterogeneity to riparian forest conditions. Heterogeneity also is added as slope gradients vary, as streams flow through constrained and unconstrained reaches, and with temporal variation in foliage cover (i.e., deciduous trees) and rainfall patterns. Unconstrained reaches and tributary junctions, in particular, are proposed as higher species diversity areas

Table 5. Primary habitat element associations of species with close ties to old-growth forest conditions.¹

Taxon	<i>n</i>	Talus	Logs	Duff/litter	Large snags	Large trees	Riparian
Amphibians	16	12	11	9	0	0	13 ²
Birds	38	0	7	0	25	10	8
Mammals	26	4	14	7	14	10	11
Total	80	16	32	16	39	20	32

¹ *n* = total number of species per taxon. Species may be represented in multiple habitat element columns. Compiled from Thomas et al.⁵¹ (includes northwestern California species).

² The former Olympic salamander is represented here as the 4 torrent salamander species.

Table 6. Habitat elements used by forest wildlife in western Washington and Oregon, as determined during the panel assessments for this book.

Taxon	Surface rock	Logs	Duff/litter	Snags	Live trees	Moss	Cavities	Shrubs
Amphibians	3	12	10	4	3	1	0	1
Reptiles	10	5	4	0	0	0	0	0
Birds	27	18	5	57	72	5	38	21
Mammals	35	50	19	22	37	4	22	11
Total	75	85	38	83	112	10	60	33

for several aquatic-dependent taxa. As habitat complexity may beget diversity, riparian forests are predictable species hotspots in western forests because they may encompass numerous habitat and microhabitat conditions.

As discussed for old-growth forests above, whereas some taxa use riparian areas for their entire lives, others are users for critical life history functions. For example, several myotis bats use riparian corridors for foraging habitat and travel corridors, but roost upslope. The terrestrial stages of aquatic-breeding amphibians may rely on riparian habitats for foraging or refuge. Assessments in Thomas et al.⁵¹ determined that 29 (36%) of 80 old-growth forest associated vertebrates were strongly associated with riparian areas (Table 5). These include 53% of the amphibians (10 species, primarily stream- and pond-breeders, and bank associates), 42% of the mammals (7 bats, Pacific shrew, shrew-mole, deer mouse, marten), and 21% of the birds (marbled murrelet, bald eagle, and 6 waterfowl species) that were assessed. As can be seen in Table 5, riparian-associated species include users of several forest habitat elements (talus, logs, snags, large trees).

Extending the diversity hotspot concept to within-landscape, forest stand-scale areas, both old-growth and riparian forests are areas of higher richness and diversity for many taxa. However, overall reduced breeding bird diversity was found along streams in comparison to upslope forest habitats by McGarigal and McComb²⁶ in the Oregon Coast Range. They suggested differences in vegetation structure and composition could explain their results: fewer large conifers and snags were noted along their study streams. More generally, riparian areas within late-successional or old-growth conditions are particularly high in wildlife numbers. An understanding of the habitat elements and microclimate components of these areas is important to fully grasp the habitat complexities of these areas. Riparian-dependent wildlife are discussed further in Chapter 13.

Habitat Elements

Several forest habitat elements are used for foraging, refuge, or reproduction by western forest wildlife. These include features such as downed logs, snags, duff or litter, and rocky substrates. They also include biotic or live vegetative components, including shrubs, live tree branches, or live remnant trees. Many of the old-growth forest associated species may occur in younger stands if these critical habitat elements are found there. Table 6 summarizes habitat elements associations for forest wildlife. Table 5 shows the primary habitat elements of old-growth associated vertebrates, compiled from Thomas et al.⁵¹ Each element in Tables 5 and 6 can be considered a dominant contributor to western forest wildlife habitats across taxa. Microhabitats provided by logs and snags, rock, duff and litter, cavities, shrubs, and large trees are key elements for forest-dwelling species. It is interesting to note that there are several differences between the results of these two assessments (Tables 5 and 6). Table 6 shows that many more species *use* these habitat elements in western forests than the more limited pool of species that are both closely tied to old-growth forest conditions and *associated* with these elements (Table 5). Criteria for use versus association are different. Among elements considered in both assessments, logs and snags were the dominant habitat elements represented in Table 5, whereas surface rock and live trees also are dominant in Table 6.

Dead and downed wood occurs in numerous forms (Figure 9). In western forests, downed wood includes logs, rootwads and stumps, wood piles and slash, roots, branches, loose bark, and bark piles. Different species tend to be associated with the different downed wood types. Among amphibians, for example, both ensatina and 57. Vega, R. M. S. 1993. Bird communities in managed conifer

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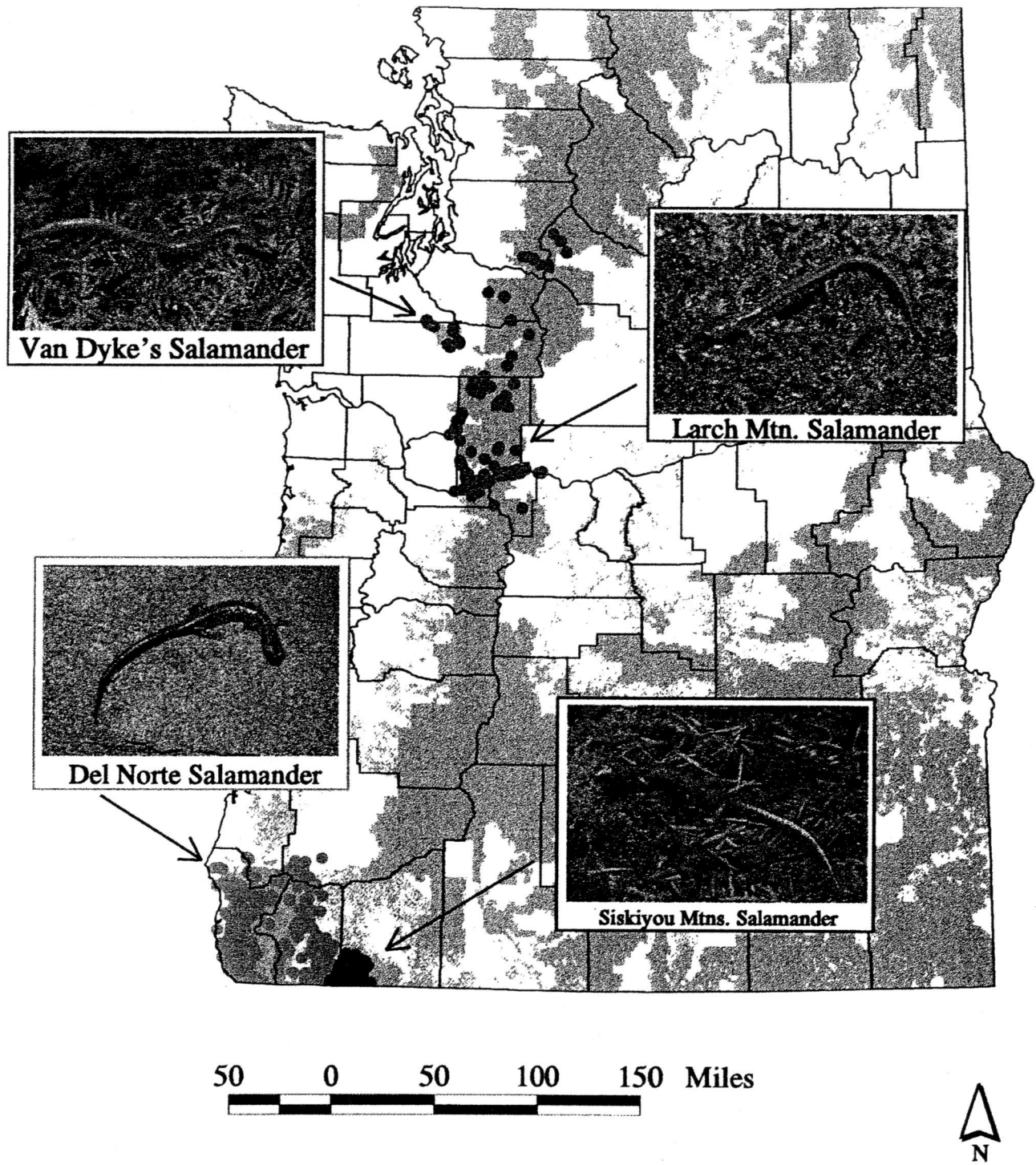
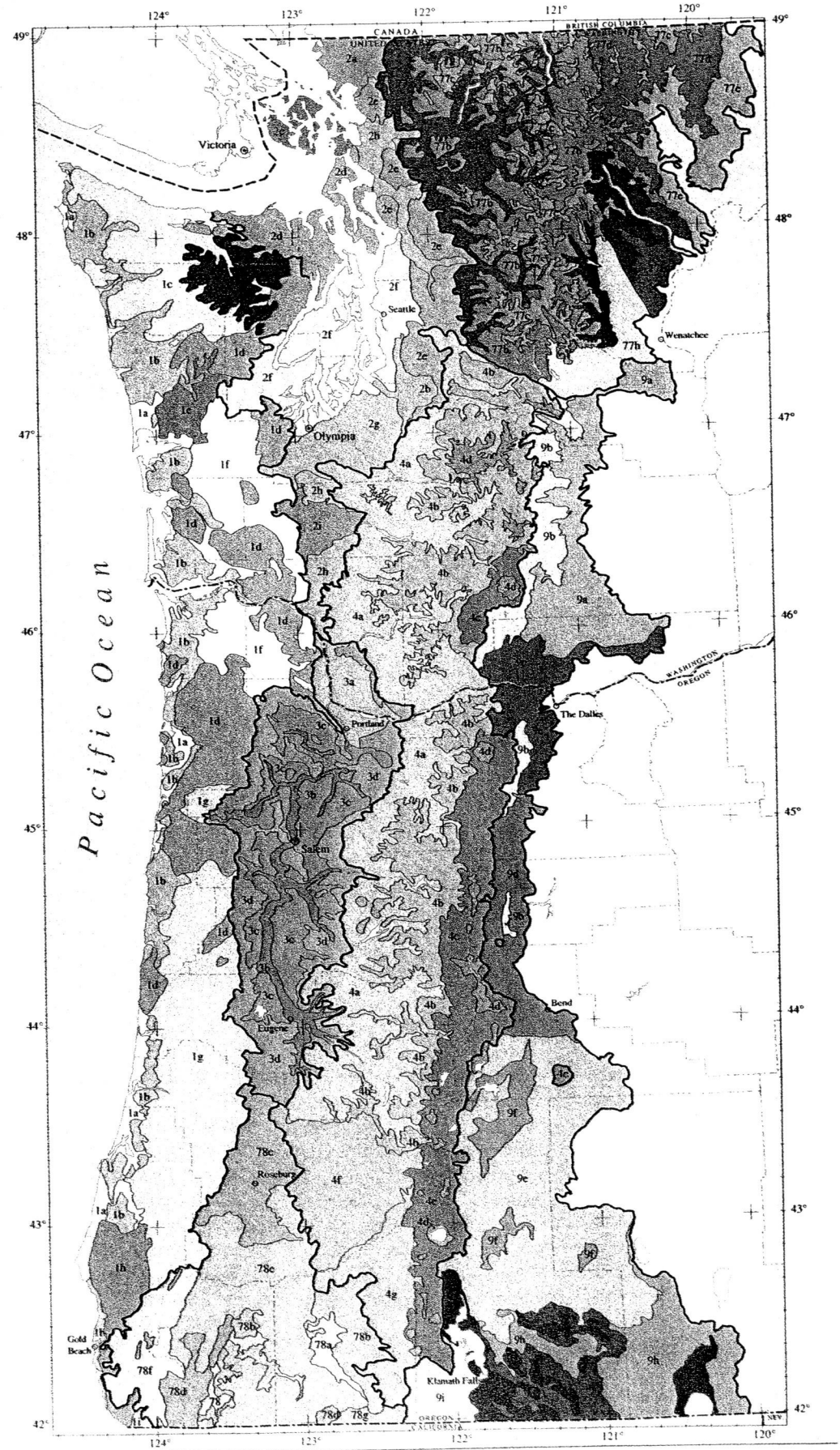
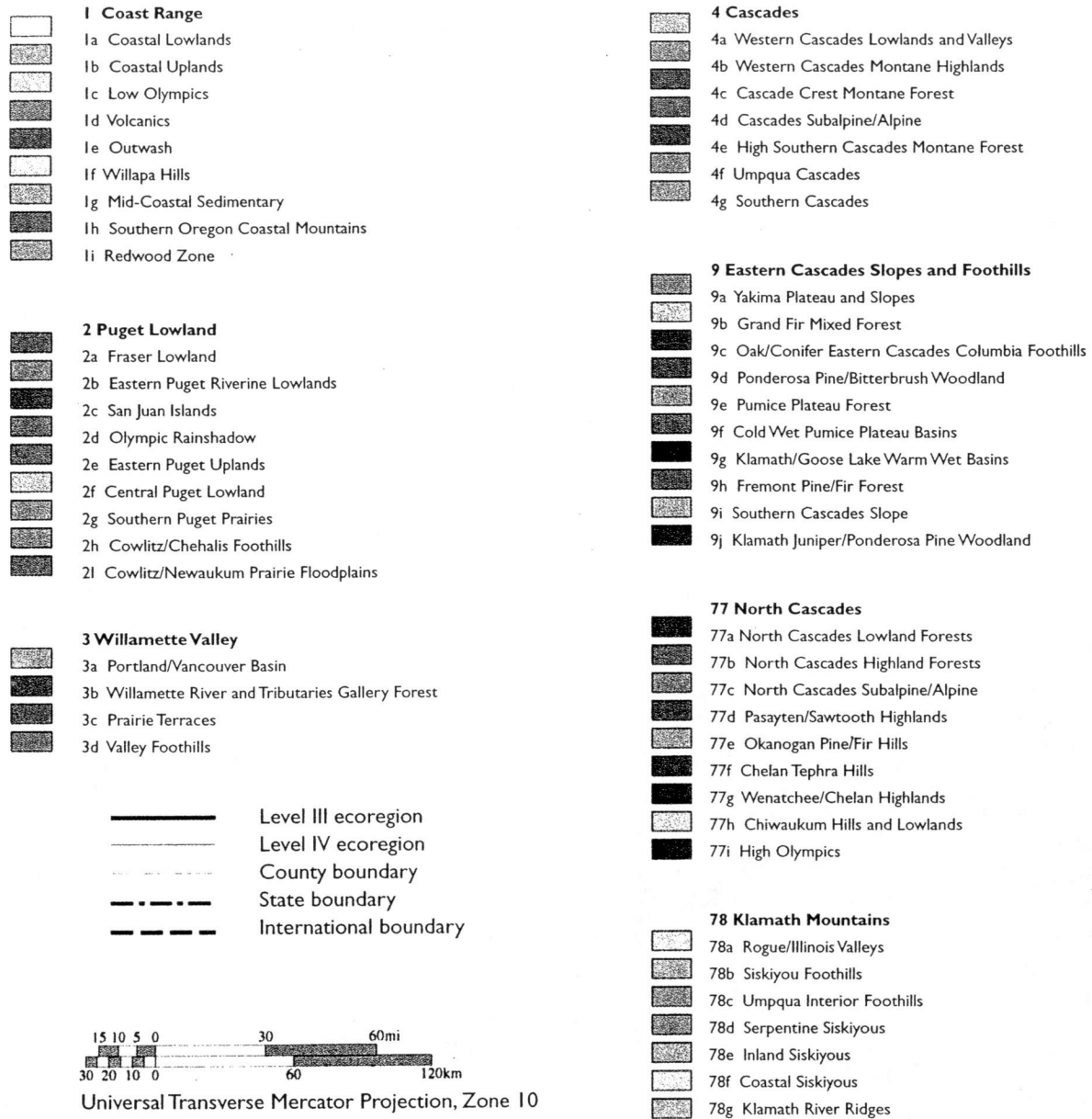


Figure 3. Four terrestrial salamanders restricted to forested habitats of the Pacific Northwest. These species are covered under the federal Survey and Manage provision of the Northwest Forest Plan, for which surveys are conducted prior to ground disturbing activities and known sites are currently managed for salamander persistence.^{34, 54, 55} W. P. Leonard, photographer. R. S. Nauman, GIS technician.

Figure 5. Level III and IV ecoregions for western Oregon and Washington, compiled at a scale of 1:250,000 by Pater et al.⁴²





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but the clouded salamander is frequently found under the bark of logs and the ensatina is often found in bark piles associated with decaying snags. Coarse woody debris, particularly large down logs, are the habitat elements most frequently used by amphibians and mammals. Large wood decays gradually, its rate dependent on the tree size, ambient conditions, and tree species. Wildlife species may have affinities for specific wood decay classes.

For vertebrates, wood provides foraging, cover, and sites for reproduction. For some species within each vertebrate class, large downed wood provides thermal refugia, buffering temperature and moisture extremes. Blessing et al.¹ demonstrated the temperature buffering capacity of a log, 20 in x 13 ft (50 cm x 4 m), containing a Van Dyke's salamander nest site. While ambient air temperatures ranged 43-76°F (6.3 to 24.7°C) in the shade 6.6 ft (2 m) from the log, temperatures inside the log cavity at the salamander nest ranged 46-63°F (7.7-17°C). For several days in the summer, the maximum nest temperature was cooler than the minimum outside air temperature. For amphibians, logs provide cool, moist, and stable microhabitats suitable for their physiological temperature and moisture requirements. Some



Figure 4. Satellite image of the Pacific Northwest. Western and montane forests are shown as darker areas on the left, and are coincident with the range of the northern spotted owl and the Northwest Forest Plan. M. Fiorella, GIS technician.

plethodontid salamander species have limited home ranges, remaining at log sites for indefinite periods. They find sufficient foraging opportunities at logs, in addition to using them for cover and reproduction. For mammals, downed wood habitats similarly provide resting, nesting and denning, and foraging habitat for numerous species (Table 6). Of the 14 log-associated mammals listed in Table 5, 2 species are bats that potentially use logs for roosting, and the remaining 12 species, 10 rodents and insectivores and 2 forest carnivores, use the downed wood for multiple life history functions. Although fewer birds rely on logs, their use of downed wood includes perching and lookout in addition to foraging sites, cover, and nesting. The sharp-tail snake is one of the few western forest reptiles associated with downed wood, and often is found in logs.

Snags are used extensively by birds and mammals (Tables 5 and 6). Cavities, cracks, crevices, and loose bark on or in snags are used by numerous species as cover and resting, roosting and nesting sites. Snag decay class is important for cavity excavators, and for species using snags for foraging. Some snag-users have preferences for snag size. Protection from predation is considered a selective force of snag use, and again, thermal buffering is thought to be a critical component of these habitat elements. Standing dead trees within intact stands will provide suitable thermal refugia for species sensitive to temperature extremes. However, some species tend to use snags in open conditions, or in a variety of closed and open forest types. Many bats have roosting and hibernacula in larger snags, some preferring snags with loose bark. Fishers use cavities for denning and resting, preferring large snags. Cavity-nesting birds include many waterfowl, owl, and woodpecker species.

Duff, litter, live trees, and surface rock are additional western forest components required by various wildlife species (Table 5 and 6). Many amphibians in western forests use duff, litter and surface rock, but only 1 species (clouded salamander, in California) has been found in trees. Rock associates include some plethodontid salamanders, such as the Del Norte salamander. Surface rock can be covered by litter and not readily identified as a likely site.³⁸ Mammals use all of these habitat elements, yet relatively little is known about the ecology of some arboreal mammals. The northern red tree vole is thought to live almost exclusively within the forest canopy. Numerous birds use live trees. Cavities and crevices are a main refuge and nesting place whereas the various canopy layers are used for foraging, cover, and nesting. Large conifers may be of particular importance to several species.

Forest Wildlife Assemblages

Sorting wildlife species by their main habitat associations helps us understand their roles in western forest ecosystems. Such assemblages or communities can be derived from the classifications of taxa relative to the habitat parameters presented here, including forest type, structural components, and habitat elements. The scale at which assemblages are identified might vary with the context that is being examined. The reptile assemblage of

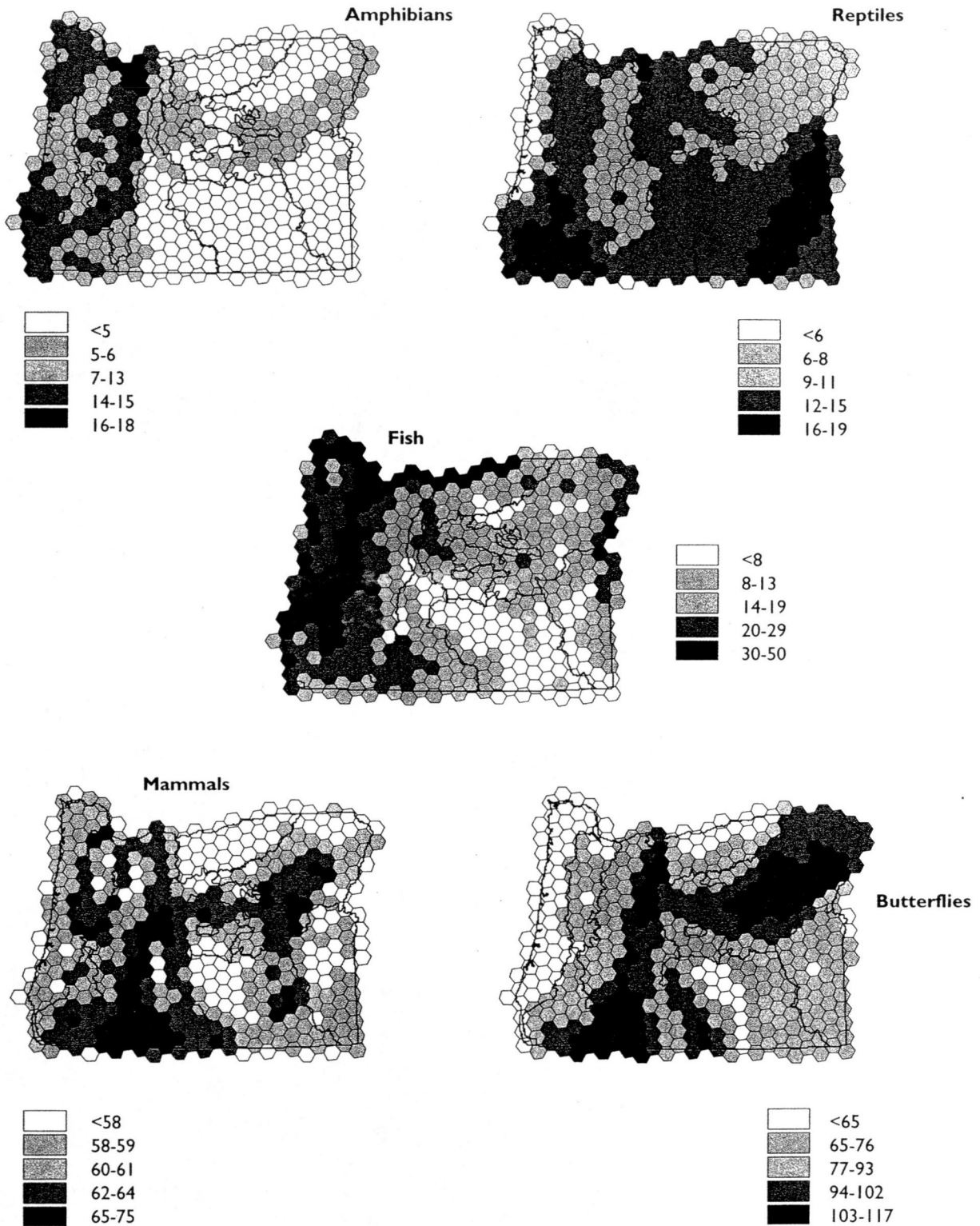


Figure 6. Species richness maps for Oregon, derived from data compiled for the Oregon Biodiversity Project⁴¹ CD-ROM. Species richness (numbers of species) categories per taxonomic group per hexagon (approximately 150,000 acres [60,750 ha]) are shown. Bird data were not available. (Courtesy of R.S. Nauman, GIS technician)

Figure 12. Satellite images of the eastern Oregon Cascade Range, showing the Three Sisters Wilderness from an eastern perspective. Upper image shows forests of the eastern Cascade ecoregion (red) and areas of downslope forest management. Lower image shows the likely impact areas of recreation (within 328 ft [100 m]) of roads and trails, focussed along riparian areas). M. Richmond, GIS technician.

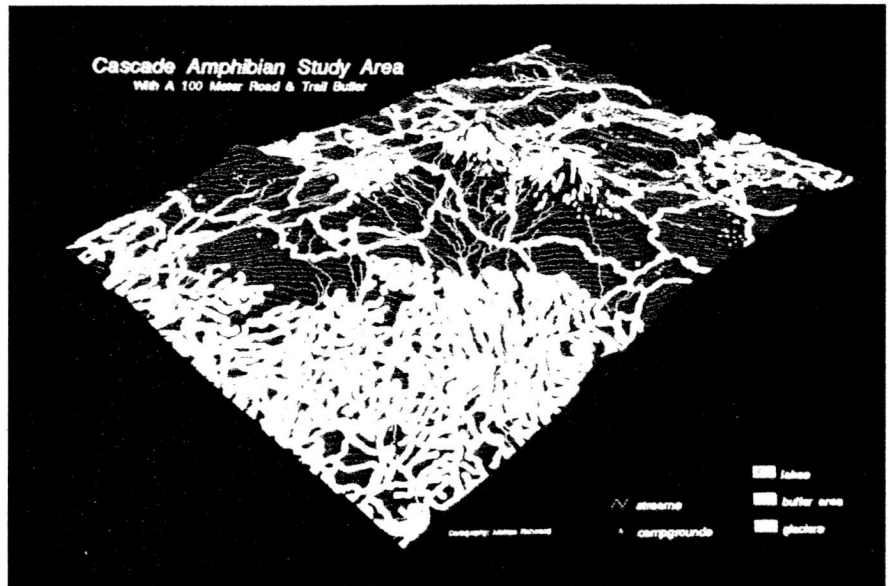
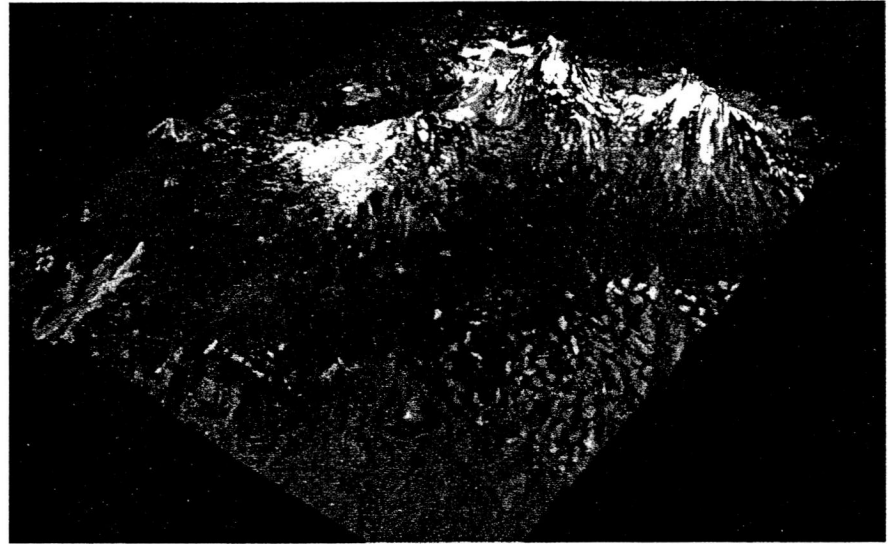


Figure 9. Downed wood provides habitat for multiple vertebrate species. H. J. Andrews Experimental Forest, western Oregon Cascades. J. Means, photographer.



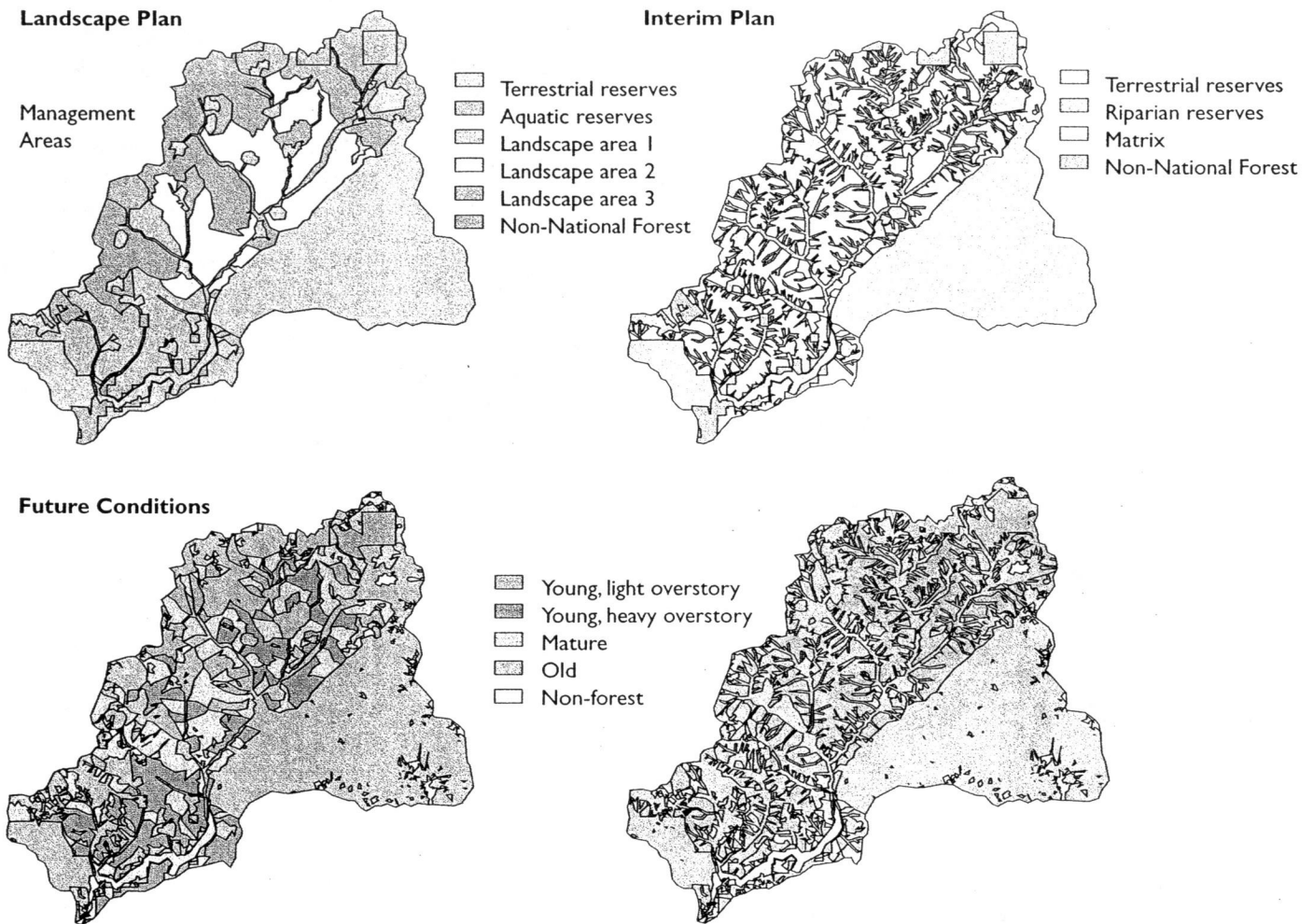


Figure 13. Management areas and projected future landscape structures for the Blue River watershed managed under Matrix and Riparian Reserve designations of the Northwest Forest Plan⁵⁴ ("Interim Plan"), and for the Blue River landscape management strategy ("Landscape Plan").¹⁴ T. Turner, GIS technician.

the Klamath ecoregion might be identified for 1 purpose, whereas in another vein Klamath woodland snakes might be distinguished. Ground-dwelling small mammals and forest canopy mammals are examples of 2 assemblages around which hypotheses of ecological function may be developed (Case History 2, below). Given the large numbers of species using snag or tree cavities, cavity-nesting species of birds and mammals is another useful assemblage in this context. Assemblages have increasing validity as distinct ecological entities when they are populated by alternative members across landscapes that span multiple species' ranges.

For amphibians, 3 main assemblages are generally partitioned for the Pacific Northwest (Figure 10). These are separated by breeding habitat: terrestrial; "pond" (inclusive of all lentic habitats; e.g., lakes and wetlands) (e.g., Figure 11); and "stream" (inclusive of all lotic waters; e.g., streams and seeps). From a finer-grained habitat

assessment of species in western and montane forests (lower portion of Figure 10), we have added complexity to this model. In western forests, distinct assemblages of stream-breeders are found in association with stream size. In headwater streams and seeps, *Rhyacotriton* torrent salamanders dominate assemblages. Cope's giant salamanders and tailed frogs may occur in some headwater channels and seeps as well. Larger downstream channels are dominated by Pacific giant salamanders, co-occurring with cottid and salmonid fishes in many systems. The stream bank community is distinct, often comprised of terrestrial-breeding Dunn's salamanders, western red-backed salamanders, and Van Dyke's salamanders. We have split the terrestrial assemblage into two groups: the rock and downed wood associates. Both groups are highly fossorial, spending much of their time subsurface. When temperature and moisture regimes at the forest surface are suitable, they can be found in

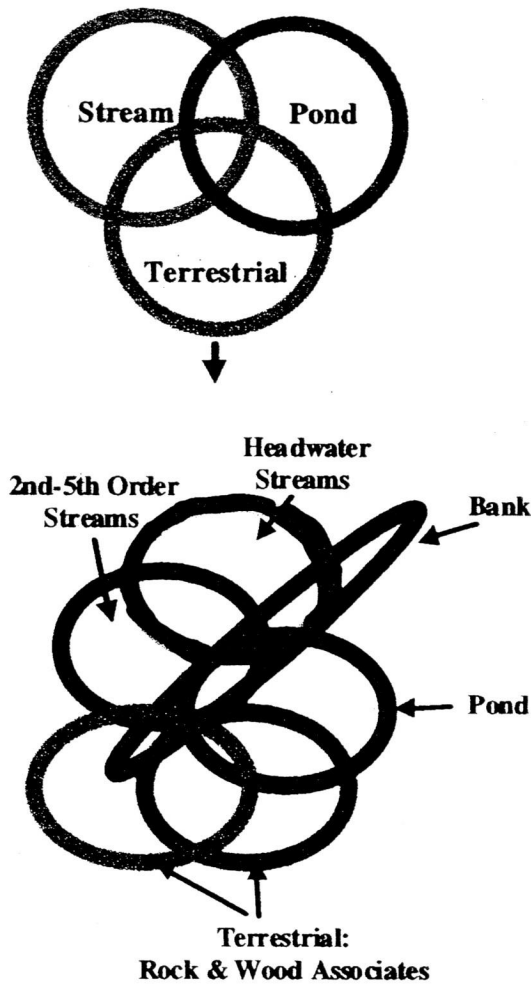


Figure 10. Fundamental (top) and finer-grained (bottom) habitat assemblages of western and montane forest amphibians.

association with wood or rock cover. At some locations, these animals may be found year-round if suitable surface refugia are available. Wood associates include the slender salamanders, the black salamander, and those species associated with logs that were mentioned previously. Rock associates include the plethodontids in Figure 3. As stream or pond breeders move into upslope forests, they often opportunistically use both wood and rock microhabitats, as well as subsurface retreats.

Overlap among assemblages is considerable for amphibians because of their complex life history. Adults are generally not restricted to breeding habitats. Thus, stream and pond breeders venture from the aquatic and riparian forest landscapes into upslope forests. Likewise, terrestrial forms occur in riparian zones and may be found streamside. The bank seems to be the primary area of assemblage overlap, as members of all assemblages are found in this near-water riparian zone. This may occur because bank conditions in western and montane forests may be almost ideally suited for amphibians, having cool moist microclimates. During summer, in particular, banks might offer surface refugia for amphibians from



Figure 11. Red legged frog (*Rana aurora*) is a pond breeder in western forests. W. P. Leonard, photographer.

inhospitable warm, dry surface conditions away from aquatic habitats. Pond-breeding amphibians such as Cascades frogs often are found along montane creeks in the summer. Foraging opportunities may be enhanced in such locations, and they may function as dispersal corridors. The relatively high species richness found along banks also might result from this being an edge between habitat types. As a boundary between habitats, you might be more likely to find members of neighboring assemblages along its interface. Or alternatively, as an edge, this region may represent a barrier to further movement.

Among terrestrial forms, rock and wood associates have the potential for relatively high habitat overlap as individuals opportunistically use cover as it is available and as suitable microclimate conditions warrant. This occurs in two ways. First, within populations, there might be use of both wood or rock, depending on its availability and suitability as habitat cover. Individuals in such populations might use the different cover types for different functions, such as dispersal cover, foraging areas, or reproduction. Dispersal cover, in particular, might be used more opportunistically. Second, for some species, there seems to be segregation of habitat use geographically among populations. For example, the Larch Mountain salamander is found in association with surface rock along the Columbia River Gorge, but is found associated with downed wood and loamy soils elsewhere.¹⁵ Similarly, the Del Norte salamander appears to be a rock associate at inland locations, and can be found with downed wood at coastal sites.³⁸ The critical factor in this might still be habitat availability and suitability. Suitable microclimate and microsite conditions for these terrestrial salamanders might occur through combinations of either of these cover types.^{15, 38}

We discuss western forest wildlife assemblages again below. First, as trophic relations are identified, assemblages may link to ecological functions and processes (see also Case History 2). Second, assemblages often are used during the development of protective measures for wildlife when forest management activities are proposed.

Species' Life History, Behavior, and Biotic Interactions

Distribution patterns of western forest wildlife are highly dependent on several aspects of their behavior and ecology. In particular, species' life history, behavior, and species interactions may need to be understood to fully explain species-habitat relations.

Dispersal limitations seem to contribute to the isolation of many amphibian populations. Amphibians generally are reliant on relatively narrow windows of temperature and moisture conditions for surface activity. Spring and fall rainy seasons are primarily when dispersal occurs for most taxa. Compounded by their relatively low mobility, amphibians' survival during migrations across heterogeneous forested landscapes can be affected. However, few studies on western forest amphibian dispersal have been conducted. Some taxa may move hundreds of feet to several miles (*Ambystoma*, *Taricha*, *Dicamptodon*, and *Rana* spp.). The terrestrial plethodontid salamanders are considered less vagile. Studies of some log-associates found movement of only a few feet over seasons to years.

A tendency for site fidelity may interact with amphibian dispersal capabilities. There may be philopatric tendencies among both the more and less mobile amphibians. Many toads known to trek miles in montane forests have high breeding site fidelity. Traditionally used breeding sites are common in pond breeding salamanders and frogs, and may occur in the other forest amphibian assemblages.

Mammals and birds seem to be less restricted in their movements (Table 3), yet many have relatively small home ranges (i.e., <10 acres [4 ha]²⁷). Even those with large home ranges may be restricted in their movements by perceived barriers on the landscape. Clearcuts and roads are suspected barriers for some species.

Interactions among species are the threads that weave the fabric of the integrated living forest ecosystem. Intraspecific interactions are often dominated by competition for food, space, and mates, and interspecific interactions involve both competition and predation. Both intra- and interspecific interactions may displace individuals or populations, affect survivorship, and result in altered distribution and abundance patterns across the landscape.

Trophic relations are established for most western and montane forest wildlife species (Table 7). Typical of food webs, most numerous among forest wildlife are the primary consumers (herbivores) and secondary consumers (primary predators). Primary consumers eat a host of plant material (e.g., leaves, seeds, sap, roots, bark, fruit). Primary consumers are birds (58% of this taxon) and small-to-large bodied mammals (e.g., rodents, deer, elk; 67% of mammals), and larval pond-breeding amphibians. Secondary consumers prey on invertebrates, vertebrates, and eggs. In western forests, some mammals, most birds and all reptile and amphibian species are secondary consumers (Table 7). Many of these are gape-limited predators that often change diet opportunistically with their size or age. Sharptail snakes are noted as feeding

Table 7. Distribution of species by trophic relationships in western Washington and Oregon.*

Taxon	Primary consumer	Secondary consumer	Tertiary consumer	Carrion feeder
Amphibians	10	29	0	0
Reptiles	1	20	0	2
Birds	96	161	6	8
Mammals	70	62	1	12
Total	177	272	7	22

* Data are compiled from expert panel assessments for this book.

on only small slugs, and most small salamanders prey on various invertebrates.

Amphibians and mammals are likely key vertebrate connectors within the western forest system. Both groups are the chief prey for secondary predators (= tertiary consumers), and as primary consumers and primary predators are conduits of energy from the lower trophic levels, particularly the diverse arthropod and fungal communities. In eastern U.S. forests, amphibians may comprise a major component of the vertebrate biomass,³ however, such a biomass estimation has not been done for western Oregon and Washington forests. Rodents comprise about half the mammal species of the region, functioning as prey for numerous species. Bats are believed to consume enormous quantities of insect prey, mainly over streams, ponds, and riparian areas. Shrews and moles are carnivorous, eating predominantly arthropods. The fungi-feeding mammals link the vertebrate trophic network with the diverse fungal community, of pivotal importance in the forest ecosystem.⁵² Fungi also are food for microorganisms and invertebrates, and have critical forest functions as decomposers, nutrient cyclers, and through their mutualistic or symbiotic relationships with other forest species.²⁸

Competition and trophic relationships are only a part of the interspecific interactions among wildlife in forests (Table 8). Wildlife mediate the reproduction of numerous forest species as dispersers or pollinators. Birds and mammals are dominant players in organismal relationships (Table 8). Their actions can alter habitats significantly, making them either suitable or unsuitable for other species. For example, cavity, burrow, and runway creators provide critical habitats for many other wildlife species.

The stability of vertebrate communities can be dependent on the balance of intraspecific, trophic, and other organismal relations with species' habitat conditions. Measures of biotic integrity attempt to determine the status of communities by assessing indicator conditions or species. These can be examined relative to disturbance impacts, such as forest management activities, to monitor forest system functions. In western forests, arboreal rodent and forest-floor small mammal assemblages are suggested to be ideal indicators of forest biotic integrity (Case History 2).

Table 8. Number of species by organismal relationships in western Washington and Oregon.*

Organismal relationship	Amphibians	Reptiles	Birds	Mammals
Controls insect populations	8	0	29	13
Controls terrestrial vertebrate populations	1	1	14	12
Pollination vector	0	0	6	0
Transportation of seeds, spores, plants or animals	0	0	65	36
Nest parasite	0	0	40	0
Creates feeding, roosting, denning, or nesting sites for other species	0	0	4	4
Creates structures	0	0	13	11
Uses structures created by other species	1	3	5	11
Cavity excavator	0	0	14	1
Cavity user	0	0	29	12
Burrow excavator	0	0	0	44
Burrow user	0	9	0	38
Runway creator	0	0	0	32
Runway user	0	0	0	33
Pirates food from others	0	0	4	0
Interspecific hybridization	0	3	12	6

* Data are compiled from expert panel assessments for this book.

Case History 2 Biotic Integrity

Andrew B. Carey

How can the effectiveness of ecosystem and landscape management be evaluated? One attractive method is to measure the integrity of select vertebrate communities.¹⁰ Ideally, these communities would consist of a limited number of year-round resident species, common enough to be found in most, if not all, patches of suitable habitat, yet sensitive enough to management that ≥ 1 species would be absent or severely reduced in abundance in unsuitable or low-quality environments. A limited number of species is desirable because operational practicality requires use of one technique of high reliability. Year-round resident species are desirable because population levels of migrants incorporate variability due to wintering and migration factors that are independent of the area being managed. Relatively high abundance is required to ensure that all species can be measured effectively when present. Two communities fit these requirements: forest-floor small mammals and arboreal rodents.

Forest-floor small mammals are interesting because complete communities with moderately high abundances of each species depends on Hutchinsonian preinteractive niche diversification—in other words, biocomplexity in the structure and processes of the forest floor. Thus, the community represents diverse forest-floor functions, abundance of coarse woody debris, and understory development. On the Olympic Peninsula in Washington, for example, the ranked relative abundances of the species in the community are Trowbridge's shrew (5), southern red-backed vole (4), montane shrew (4), deer mouse (4), forest deer mouse (3), shrew-mole (3), creeping vole (3), and vagrant shrew (2). Assemblages in other provinces

are listed in Carey and Johnson.⁸ This community can be described with various techniques: live trapping, pitfall trapping, and snap trapping.

Another interesting community is the arboreal rodent community. In Washington, the community consists of northern flying squirrel, Douglas' squirrel, and Townsend's chipmunk. In Oregon, one has the option of adding bushy-tailed woodrat, dusky-footed woodrat, and red tree vole. Individually and collectively, the biomass of these species is indicative of carrying capacities for a variety of vertebrate predators including mustelids, hawks, and owls. In addition, in managed forests, community arrangement will diverge from the high abundances of all members found in old growth, to communities dominated by 1 or 2 species when management has failed to adequately address key ecosystem components.⁶ In particular, the arboreal rodent community measures ecological productivity—the energy that the system of fungi, understory plants, and overstory trees diverts to reproduction (truffles, mushrooms, fruits, seeds, and nuts). This community integrates production of fruit with the decadence process that produces cavities and affects spatial arrangements of habitat elements. This results in niche diversification. Thus, the sum of the population sizes of species in the arboreal rodent community measures, in large part, the energy the system is putting into reproduction.⁹ This community (with the exception of red tree vole) can be effectively described with live trapping.⁵

Arboreal rodents and forest-floor small mammals can be used both to monitor effectiveness⁶ but also to predict results of forest management strategies through modeling.¹⁰ The use of biotic integrity, when supported by basic research, offers an alternative approach for populations of rare, cryptic, or other species that are difficult to study, survey, and manage.

Management Issues

Western and montane forest management policies in Oregon and Washington are undergoing tremendous changes, largely to address the long-term persistence of species and to ensure the maintenance of ecosystem integrity. The main human uses of western and montane forests include timber production, water resources, special forest products, recreation, mining, and the associated support systems of roads and trails (Figure 12, page 202). These forests also maintain the treasuries of biophysical legacies, functions, and processes having aesthetic, ethical, and cultural values within our society. However, across this landscape, timber management has been the dominant focus on both public and private lands for >100 yrs. By the 1970s and 1980s, concern for high profile species such as the northern spotted owl grew as late-successional and old-growth forests were diminished and fragmented because of logging, and as the U.S. Endangered Species Act (ESA) of 1973 prohibited harm to species listed under the Act, and to their habitats. Studies were initiated to understand main habitat associations of the northern spotted owl, as well as the requirements of numerous other suspected obligates to the ancient forests of this region. By 1994, >1000 taxa were identified as likely associates of old-growth forest habitats.

Federal Forest Management

The range of the northern spotted owl has close resemblance to the western and montane forests considered in this chapter (Figure 4), but also extends latitudinally beyond Oregon and Washington. In the U.S., 42% of this landscape is federally administered (24.3 million acres [9.8 million ha]⁵³). This landscape across 3 states was used to develop the first ecosystem management plan for the nation which spanned land ownerships: the federal Northwest Forest Plan.⁵⁴ The Plan's goals included providing for the highest contribution to the socioeconomic needs of the region while ensuring the long-term viability of the old-growth forest ecosystem and associated species. Although the Plan has been in place for 6 years, the balance of socioeconomic productivity and protection of biological integrity is a challenge that is still being developed as we enter the 21st century. The Plan is based on adaptive management, and thus the adaptive phase is expected to continue as new knowledge and management tools develop for western forests.

For species protective measures, the foundation of this Plan relies on several land allocations, habitat provisions, and species-specific mitigations.⁵⁴ A backbone of reserved lands was created across the region for the maintenance of well-distributed populations of most of the broad ranging taxa considered. For habitats of fish and riparian-dependent species of concern in the region, an Aquatic Conservation Strategy^{45, 54} was formulated, including protections of key watersheds, development of watershed analysis, watershed restoration, and identification of Riparian Reserves, primarily along streams and around unstable areas. Forest habitat provisions included coarse

woody debris management, specified snag and green tree retention levels, and forest management for red tree vole and northern spotted owl dispersal corridors. For species that were not adequately protected by these series of measures, a "Survey and Manage" provision was created.^{53, 54, 55} For those of the most concern, sites proposed for ground disturbance would be surveyed for the species of interest, and if found, managed to maintain the persistence of that species^{54, 55} (Figure 3). These protection measures are additive, together addressing the long-term persistence of old-growth associated species on the federal forest landscape in this region.

Since implementation of this Plan, alternative landscape management plans have developed. The measures developed for the Northwest Forest Plan might be considered experimental, since nothing of that scope has ever before been attempted in this region. The Plan may not be the sole means to maintain ecosystem integrity and biological legacies in western forests, while also providing timber products and other socioeconomic values. For the federally administered Augusta Creek watershed, an alternative scenario of forest management was developed using the natural disturbance processes (i.e., fire) of the landscape as criteria for forest management.¹³ Forest rotations and green tree retention levels were matched to fire frequency intervals (100, 200, and 300 years) and intensities (15-50% retention). The Plan's Riparian Reserve system was reduced to provide buffers along only the mainstem fish-bearing streams; however, tree retention would be weighted along other stream channels in harvested units. Aquatic reserves also were placed in small basins for species or areas of concern. The resulting landscape was modeled and evaluated after several hundred years and found to have advantages over the Northwest Forest Plan landscape at the watershed scale. Importantly, the fragmented and edgy "spaghetti" landscape of the Plan (i.e., spatial pattern resulting from the highly dendritic stream network and its accompanying Riparian Reserves, between which harvested units are located) is consolidated into larger contiguous forest blocks. Benefits for wildlife included improved habitat connectivity and maintenance of interior old-growth conditions in much of the landscape because of reduced edge effects on microclimate.¹² This scenario, with some adjustments, is being tested in a neighboring watershed of the Willamette National Forest in the western Oregon Cascade Range (Case History 3).

Case History 3

The Blue River Landscape Study

John H. Cissel and Frederick J. Swanson

A team of scientists and managers working on the H. J. Andrews Experimental Forest and the Blue River Ranger District of the Willamette National Forest have been cooperating for most of this decade to develop and test a landscape management approach based on natural disturbance regimes.^{13, 14} The team has been motivated to

a significant degree by concern over the loss and fragmentation of older forests, and the lack of a coherent long-term strategy for conservation of older forest systems in managed landscapes. The underlying assumption of this approach is that by approximating key aspects of important disturbance regimes in management regimes, risks posed to native species and ecological processes are reduced as compared to other historical and contemporary landscape management approaches.^{23, 29, 49}

The Blue River Landscape Study is intended to evaluate the potential effects of implementing a landscape plan based on historical landscape dynamics. The landscape management approach used in the study is intended to meet the same general objectives underlying the Northwest Forest Plan:⁵⁴ provide habitat to sustain species associated with late-successional forests, maintain and restore aquatic ecosystems, and provide a sustainable supply of timber. A combination of effectiveness monitoring, long-term plots, retrospective studies, and modeling assessments are being used to evaluate and adjust this landscape management approach. The Blue River watershed provides an ideal setting for the study due to its size (approximately 56,790 acres [23,000 hectares]) and the presence of the H. J. Andrews Experimental Forest and numerous long-term studies within the watershed. In addition, the Blue River watershed is a part of the Central Cascades Adaptive Management Area, a federal land allocation in the Northwest Forest Plan that encourages development and evaluation of new approaches.

The dynamics of historical landscapes in this area were heavily influenced by fire of varying frequency, severity and spatial extent. General patterns of past fire behavior were interpreted into three fire regimes based on a 500-year dendrochronological record.^{33, 50, 58} For example, wet, cool sites burned infrequently while warmer, drier sites burned more frequently. Characteristics of these three regimes were used to establish timber and fire management regimes in actively-managed portions of the landscape. Timber harvest frequency and rotation age (100-260 years) were based upon historical fire frequency, timber harvest intensity (15-50% overstory canopy retention) was based upon historical fire severity, and the spatial patterns of timber harvest were based upon the spatial patterns of historical fires. Implementation guidelines are intended to reflect natural disturbance patterns to the extent feasible while protecting ecological values.

An aquatic reserve system also was established to help meet the aquatic ecosystem objectives in the Northwest Forest Plan.^{45, 54} These reserves are of two types: small-watershed reserves and corridor reserves. Small-watershed reserves are strategically located throughout the watershed to encompass areas of particular importance to aquatic ecosystems and spotted owls. In addition, corridor reserves are established on all fish-bearing streams. Figure 15 depicts the landscape management plan ("Landscape Plan"), and, for comparison, a literal

implementation of the Northwest Forest Plan as if it were applied to the Blue River watershed ("Interim Plan"; e.g., Riparian Reserves occur on all streams, and 80-year rotation regeneration harvests with 15% retention occur in the "Matrix"⁵⁴).

A watershed restoration strategy is an integral component of the Blue River landscape management approach. Restoration activities are intended to reestablish a resilient, interconnected aquatic network capable of maintaining aquatic habitats and processes while management activities are occurring in the watershed. Road restoration activities are planned to occur first in areas where risks to aquatic ecosystems are high.

Future timber harvest and forest successional patterns were projected across the watershed for the next 200 years for both plans (Figure 13, page 203) and analyzed. Results show that the landscape plan will produce more late-successional habitat (71% of the watershed versus 59%) in a less fragmented landscape as compared to the interim plan.¹⁴ Larger patches in the landscape plan create more interior habitat, thought to benefit some wildlife species such as the northern spotted owl. Less edge between old and young forests in the landscape plan reduces edge effects such as altered microclimates and increased plant mortality, and may reduce habitat for certain species that favor edges, such as elk. More complex stand structures are present in the landscape plan due to generally higher overstory canopy retention levels. Retention of live and dead trees in young stands has been found to favor cyanolichens, certain fungi and invertebrates associated with older forests, amphibians with life histories requiring both stream/riparian and upland habitats, provide more options for protection of rare species, and to moderate understory environments. The landscape plan also maintains a substantial component of mature forest (80-200 years old). In contrast, the interim plan nearly eliminates the mature forest component because almost all lands are either in a reserve, where all stands grow old and large-scale disturbance is eliminated, or in matrix lands where a relatively short rotation (approximately 80 years) prevents regrowth of mature forest. We feel that the absence of mature forest in the interim plan poses substantial risk when mortality due to disturbance, climate change or senescence eliminates older Douglas-firs in the reserves.

Landscape structures resulting from both the landscape management plan in this study¹⁴ and from the interim plan are historically unprecedented. For that reason we feel it is critical that an adaptive management approach be followed for both plans. We are pressing ahead with implementation, monitoring, modeling, and research to better define and evaluate a historically-rooted approach in the Blue River watershed based on the landscape dynamics inherent to the area. We hope these concepts can be tested in other provinces in the region, and that the Matrix and Riparian Reserve approach of the interim plan⁵⁴ can be similarly tested.

57. Vega, R. M. S. 1993. Bird communities in managed conifer stands in the

State and Private Forest Management

In the last decade, several forest management plans at watershed to landscape scales have been designed by state agencies and industrial land owners. These alternative approaches to forest management reflect the diverse alignment of roles as wildlife stewards of these land owners. On federal lands, the more conservative standard has been set for species maintenance or restoration as a priority equal to or greater than providing economic returns. On state lands, timber revenue is an identified priority, and consequently a more intensive timber management program is implemented. Although species persistence is addressed by states and many rare species protective measures are implemented, a relatively greater risk to native habitats and species is perceived with their more intensive timber harvest practices, reduced reserved lands, and narrower riparian buffers. Whether or how states might alter their role as ecosystem and biodiversity stewards is currently a debated issue regionally and nationally. Private and industrial forest land owners seek to maximize timber returns, and while they actively design provisions to maintain biodiversity as legally required, their provisions may minimally protect species habitats, rarely identify all taxa associated with the forest landscape, and do not necessarily restore habitats to allow rare species to [re]colonize their lands. Industrial land owners with more extensive land holdings have been more proactive for species protections, yet on the broader spectrum, they seem to be held less accountable for species persistence than state and federally administered lands. Although there is acknowledgment of the different roles of land owners for ecosystem, habitat or species stewardship, a good model for a managed alignment of these diverse roles has not been developed for a landscape with multiple ownerships. The "Coastal Landscape Analysis and Management System" project is hoped to advance such a model for the Oregon Coast Range province.⁴⁷

Standards for species and particularly wildlife conservation are changing and we are still mid-pivot. "Precautionary principles" are more often cited as rationale for conservative forest management decisions, and there has been a shift in the burden of proof for species and habitat protections: we've gone from needing to prove a value needs protection before providing it, to proving it has adequate protection before lifting it.³⁶ As mentioned above, there also has been a switch from addressing a few threatened and endangered wildlife species to a broader spectrum of species (e.g. fungi, lichens, bryophytes, mollusks) and assemblages (e.g. arthropod functional groups).^{53, 54, 55} Increased public concern and review add complexities to processes that now seem to require full consensus, whereas they were more authoritatively controlled previously. Litigation or the threat of litigation has been an effective driver of these changing land management ethics. As adaptive management approaches are being advocated, long-term contracts for state and private Habitat Conservation Plans are becoming more and more difficult to achieve. And finally, while the policy arena is embroiled in controversy over how much wildlife

protection is needed in different portions of the western forest region, by ownership and location, the science of forest management is rapidly changing.

Sustainable forestry techniques currently being tested across western Oregon and Washington forests are numerous and innovative. Forest density management and alternative silviculture is being examined for both restoration and regeneration harvests by interagency collaborative partners. Selective harvests are being more broadly implemented. Mosaics of thinning levels, clearcut islands, and green tree leave islands may achieve multiple forest objectives, retaining localized patches of rare species or species hotspots while opening other patches for regeneration of shade intolerant tree species and production of greater wood volumes. Such practices are more costly, involving greater site reconnaissance and site preparation, and more complex logging directions, but they also may attain goals for compatible wood production and biological resource protection at the site level. The role of leave islands for vertebrate species persistence within a managed forest landscape needs further study.

Several forest management approaches and provisions are being tested, or are in need of being tested. Riparian management approaches are being examined at the site level. Alternative stream buffer widths are being examined (e.g., Figure 14). Concurrently, forest biological resources are being investigated. Are there habitats or taxa that require special consideration in various portions of the stream network? If so, what are their responses to alternative forest management designs? Stream buffers may not be the only mechanism for aquatic and riparian resource maintenance. Those in current use do not provide interior old-growth microclimate conditions along streams, but rather mitigate for slope slippage, water temperatures, wood inputs to streams, or perhaps development of late-successional structural components (e.g., large tree size). Patch reserves along streams have been proposed but not tested. Patches and buffers might be used together, like beads on a string, to provide intermittent riparian habitats with interior conditions and narrower intervening sections designed to retain stream temperatures, limited downed wood recruitment, and near-stream habitat.

Management of downed wood recruitment is another topic in need of additional attention. As presented in this chapter, many wildlife habitat associations rely on dead and downed wood. Yet are we maintaining and managing for the recruitment of sufficient large logs and snags? Examination of log decay classes in managed forests reveals a paucity of hard logs, and in some locations, mostly just legacy large wood from high-grading harvests of half a century or more ago. Loss of coarse woody debris has implications for mammals and amphibians, key taxa in food webs, linking producers to consumers.

Spatial scale of protection is an issue that needs to be addressed for multiple wildlife species and habitats across Oregon and Washington. What resources should be maintained at the site, at the watershed or land-ownership block, or at the landscape and region? Is the intent to

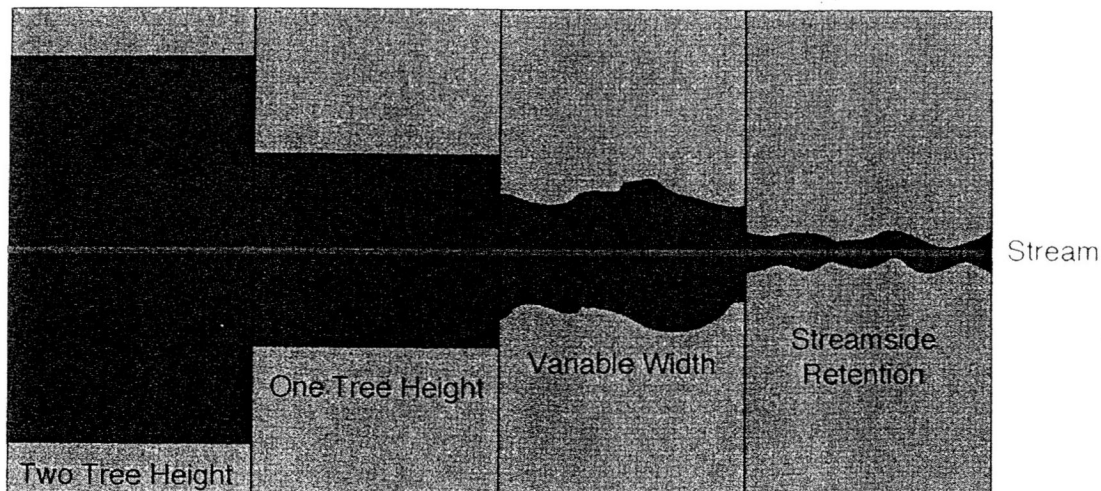


Figure 14. Alternative riparian buffer widths being examined in headwaters, with upslope density management. Tree heights correspond to federal interim Riparian Reserves for the Northwest Forest Plan.⁵⁴ The variable buffer has a 50-foot (15 m) minimum and varies with topographic or vegetation conditions, and the streamside retention buffer retains only

streamside trees for bank stability, those within about 20 feet (6 m) of the stream (D. Olson, Riparian Buffer Study, interagency research conducted by the Bureau of Land Management and the U.S. Forest Service in western Oregon forests). K. Ronnenberg, graphics artist.

maintain all rare species and key habitats at all localities? At what level of rarity can sites be prioritized for maintenance at larger scales, such as a watershed or land ownership, so that losses at individual sites are acceptable if larger scale persistence is assured? What levels of risk are acceptable for these different species-rarities, habitats, and spatial scales? Can protective mitigations be nested among sites, watersheds, provinces, landscapes, and ownerships? Mechanisms and processes for multiscale and inter-landowner management approaches need advancement. These need to be tied to effective monitoring strategies and adaptively managed.

Conclusion

Several common themes are presented for new directions in western and montane forest management. These are sure to develop further in the next few years and decades.

1. The burden of proof is shifting to demonstrable stewardship of species and their habitats prior to implementation of west-side forest management activities, with increased use of the "precautionary principle" and conservative approaches to hedge uncertainties and risk to species persistence. Increased public involvement and oversight forest land management activities is partly responsible for this trend, resulting in greater land-owner accountability for the maintenance of natural resources.
2. Well-defined goals are needed for wildlife management in western forests among federal and state agencies, private and industrial land ownerships.

3. Integrated habitat-based and species-specific management approaches are being designed by federal, state, and private landowners.
4. Collaborative efforts are being initiated to investigate alternative management approaches to achieve multiple resource production and protection across landscapes.

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