

Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review

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Abstract

Non-coniferous vegetation, including herbs, shrubs, and broad-leaved trees, makes a vital contribution to ecosystem function and diversity in Pacific Northwest conifer forests. However, forest management has largely been indifferent or detrimental to shrubs and trees that have low commercial value, in spite of a paradigm shift towards more holistic management in recent decades. Forest management practices that are detrimental to broad-leaved trees and shrubs are likely to decrease habitat diversity for wildlife, but the number of species that may be affected has not previously been enumerated. I reviewed life history accounts for forest-dwelling vertebrate wildlife species and derived a list of 78 species in Oregon and Washington that are associated with non-coniferous vegetation. The diversity of direct and indirect food resources provided was the primary functional basis for associations of most species with non-coniferous vegetation. Thus, a diversity of herbs and broad-leaved trees and shrubs provides the foundation for food webs that contribute to diversity at multiple trophic levels in Pacific Northwest conifer forests. Given the number of species associated with non-coniferous vegetation in conifer-dominated forests, maintaining habitats that support diverse plant communities, particularly broad-leaved trees and shrubs, will be an important component of management strategies intended to foster biodiversity. Silvicultural practices such as modified planting densities, and pre-commercial and commercial thinning, can be used to control stand density in order to favor the development of understory herbs, shrubs, and a diversity of tree species within managed stands. Allowing shrubs and hardwood trees to develop and persist in early seral stands by curtailing vegetation control also would benefit many species associated with non-coniferous vegetation.

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1. Introduction

Management and research of forest ecosystems has been mainly preoccupied with overstory trees, particularly conifers, since they are dominant structures and represent a major portion of the economic value of forests. Consequently, past forest management practices in the Pacific Northwest have emphasized conifer establishment and dominance, often to the detriment of other vegetation. Early, shrub-dominated stages of forest succession, which typically support higher animal diversity than other stages (Harris, 1984; Hall et al., 1985), have been truncated by management practices that promote early establishment of conifers on forestlands managed for timber production (Hansen et al., 1991). Vegetation management and narrow spacing of conifer seedlings serve to reduce competition from other species (Walstad and Kuch, 1987),

producing young, closed-canopy second-growth across thousands of hectares in the Pacific Northwest. This forest condition is productive from a timber management perspective, but the homogeneous structure supports low diversity of wildlife (Hayes et al., 1997).

In the past decade, management objectives for public forests in the Pacific Northwest have expanded beyond simply achieving commercial goals, to encompass a broad suite of resources and ecosystem functions, including native biodiversity. Along with this paradigm shift, recognition of the contribution of non-coniferous vegetation to biodiversity and ecosystem function has been increasing. Herbs, shrubs, and broad-leaved trees not only represent a large portion of the plant diversity in Pacific Northwest forests (Halpern and Spies, 1995), but also have important ecosystem functions, including nutrient cycling, carbon sequestration, and contributions to soil fertility (Nilsson and Wardle, 2005; Chastain et al., 2006). Broad-leaved tree species, such as red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*), also function in nutrient cycling, and influence soil fertility, aquatic food webs, and

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wildlife habitat (McComb, 1994; Bunnell et al., 1999; Compton et al., 2003; CFER, 2005). Furthermore, non-coniferous vegetation is a source of structural complexity at multiple spatial scales. Structural complexity contributes to the maintenance of biodiversity by providing a diversity of habitat niches for organisms (Carey, 2003; Lindenmayer et al., 2006). At the scale of forest stands, the presence of non-coniferous habitat elements such as broad-leaved trees and shrubs has been associated with richness and/or abundance of bird (Huff and Raley, 1991; Hagar et al., 1996; Willson and Comet, 1996a, 1996b), herpetofaunal (Gomez, 1992), and mammal communities (Carey and Johnson, 1995; Gomez and Anthony, 1996) in northwest forests. Patches of non-coniferous vegetation on the landscape, such as seral stands of shrubs, alder, cottonwood, or aspen, provide unique resources that contribute to beta diversity. Non-coniferous vegetation makes significant contributions to structural and compositional diversity throughout all stages of forest development.

In spite of a paradigm shift to more holistic ecosystem management of forests, current policies and practices still tend to overlook the importance of non-coniferous vegetation in meeting goals related to sustainability and biodiversity. State and federal reforestation standards continue to promote conifer dominance by specifying minimum stocking densities of commercially valuable tree species and limited time frames within which seedlings must be “free to grow” (out-competing other vegetation; Adams, 1996; Washington DNR, 2005). These standards apply to forests burned by wildfire as well as to harvest units. In addition, a current focus of management on federal (USDA and USDI, 1994) and state lands (McAllister et al., 1999) is the restoration of old forest structure, primarily emphasizing the large-tree component of these forests. This approach is in danger of neglecting both early seral stages dominated by shrubs or deciduous trees (Kennedy and Spies, 2004), and the non-conifer understory components of mature forests. Although much of the concern in recent decades over threats to biodiversity has centered on loss of old-growth forest habitat, floristically diverse early seral stages, which can support a very high diversity of plant and animal species (Harris, 1984; Hall et al., 1985), also are jeopardized by forest practices that promote rapid conifer dominance after disturbance (Hansen et al., 1991). Finally, conversion of hardwood-dominated riparian areas to conifers may have negative consequences for some hardwood-associated species, and for biodiversity in general, but these effects have not been well studied (CFER, 2005). As a result of these and other management practices, shrub and hardwood tree cover, in at least some parts of the Pacific Northwest, has declined over the past five decades (Kennedy and Spies, 2004). Loss of non-coniferous vegetation from coniferous systems poses a threat to biodiversity (Bunnell et al., 1999; Koivula et al., 1999; Hanley, 2005).

Although there is general recognition that achieving diversity goals for wildlife requires managing for a diversity of habitats, there seems to be a lack of clarity regarding interpretations of “structural complexity” and “understory vegetation”. Terms such as “vertical and horizontal hetero-

geneity”, “structural complexity,” and “biocomplexity” have been used to describe conditions of forest stands that are desirable for fostering faunal diversity (Carey, 2003; Lindenmayer et al., 2006). But definitions for these concepts that would allow managers to translate them into on-the-ground practices at appropriate spatial scales are needed. Foresters often use the term “understory” to describe regenerating conifers, whereas other vegetation is referred to as “brush” (as demonstrated by a search for the term “brush” on the Society of American Foresters webpage). Thus, silviculturists may encourage the development of understory conifer seedlings and saplings when implementing plans to increase stand structural diversity (e.g., Newton and Cole, 2006). But few studies have addressed whether a forest stand that has multiple layers of coniferous foliage would support as diverse a wildlife assemblage as one with non-coniferous vegetation occupying mid- and understory layers. More explicit information on the elements of stand compositional and structural complexity that are important in meeting the habitat requirements of forest-dwelling species would help managers draft prescriptions for promoting biodiversity.

In this paper, I provide a review of habitat associations of terrestrial vertebrates with non-coniferous vegetation in Pacific Northwest conifer forests. Although habitat associations vary regionally, the contribution of a diverse flora in supporting a diversity of wildlife has been recognized for various forest types throughout the Pacific Northwest (Bunnell et al., 1999). I primarily focus on moist and montane forests in Oregon and Washington as examples of regions where forest management effects on non-coniferous vegetation are likely to have an important influence on wildlife diversity. Information on wildlife associations with habitat that is specific to a region can assist managers in refining strategies for maintaining biodiversity. While many studies have documented associations of individual species with broad-leaved trees, understory shrubs, ferns, herbs, or other vegetation, a compilation of the existing data is needed to emphasize the importance of these habitat elements based on the diversity of wildlife species they support. Bunnell et al. (1997) provided a brief overview and extensive list of terrestrial vertebrate species that use broad-leaved tree and shrub habitats in Oregon, including species that are not closely associated with conifer forest habitats. My emphasis in this paper is different because I wanted to provide information on habitat associations with non-conifer vegetation in both Oregon and Washington, and to highlight the species most likely to be affected by forest management. Therefore, the information I compiled in this paper focuses on species for which conifer forests provide primary habitat. Another goal of this review was to explore the functional bases underlying species associations with particular types of vegetation.

2. Methods

To derive a comprehensive list of species associated with non-coniferous vegetation, I queried the database compiled by Johnson and O'Neil (2001) for species associated with shrub

layer, percent shrub canopy cover, flowers, lichens, herbaceous layer, ferns, forbs, and fruits, seeds, and nuts in forests of Oregon and Washington. I also searched the comments accompanying species that were categorized as associated with the habitat element “trees” to find evidence for any special associations with non-coniferous tree species. For each species on the resulting list of those associated with non-coniferous vegetation, I performed a literature search for additional information about the functional bases underlying habitat associations. I relied primarily on species accounts that summarized information from multiple studies (Verts and Carraway, 1998; Marshall et al., 2003; Poole, 2006).

An objective of this paper was to draw attention to species whose populations may be jeopardized if adequate non-coniferous habitat is not provided in managed forests. Species that are associated with non-coniferous vegetation and that also have declining, insecure, or uncertain population status may be of the greatest concern to managers. Therefore, I researched the legal and conservation status of each species by consulting the Natural Heritage database (NatureServe, 2006) and lists of endangered, threatened, and special-status species available at websites maintained by Oregon’s and Washington’s Departments of Fish and Wildlife. Population trends for bird species on the list were compiled from Breeding Bird Survey (BBS) data (Sauer et al., 2005) for Oregon, Washington, and the Southern Pacific Rainforest and Cascade Mountain physiographic strata (Ruth, 2006). State level BBS data represent bird population trends across all habitats in which each species occurs in each state. BBS data from the two physiographic strata also are considered because they represent population trends in regions within the two states that are most likely to be affected by forest management. Populations of some species that use non-coniferous habitat elements but primarily occur in or are abundant and widespread in non-forested habitats (e.g., American robin (*Turdus migratorius*), raccoon (*Procyon lotor*)) are less likely to be critically influenced by forest management and were not included on the list.

3. Results

My review of habitat associations for wildlife species that occur in forested habitats indicated that at least 78 terrestrial vertebrate species (1 amphibian, 1 reptile, 39 birds, and 37 mammals) use non-coniferous vegetation in conifer-dominated landscapes in Oregon and Washington (Table 1). Twenty-one bird and three mammal species are associated with non-coniferous vegetation for both food and cover. The use of non-coniferous vegetation was primarily related to food resources for 9 bird and 26 mammal species. No species were associated with non-coniferous vegetation for cover alone. Although there was substantial evidence of associations with non-coniferous vegetation for seven species (black-throated gray warblers, Baird’s shrew, Pacific shrew, montane shrew, vagrant shrew, Trowbridge’s shrew, and hoary bat (scientific names of vertebrates associated with non-coniferous vegetation are given in Table 1)), no underlying functional bases for these relationships have been documented.

Nine species (one amphibian, three birds, and five mammal species) have a special federal or state status (Table 1). Loss of habitat as a result of forest management practices that influence the availability of non-conifer habitat elements is listed among the threats to five of the special-status species (mountain quail, willow flycatcher, western bluebird, Columbian white-tailed deer, and western gray squirrel). Mountain quail populations in coastal Oregon and Washington are relatively stable, but elsewhere have experienced range contractions caused by loss of woody vegetation associated with riparian habitats, loss of upland shrub habitats, loss of plant species diversity, and simplification of habitats (USFWS, 2003). Major threats to the willow flycatcher include factors that destroy or degrade shrubby vegetation. Willow flycatchers breed in riparian habitats throughout the arid and agricultural west, but nest success can be higher in early seral conifer forests that support dense cover of deciduous shrubs (Altman, 2003). Local declines of western bluebirds have been primarily related to reduction in availability of nest sites, including dead trees created during natural disturbances such as fire. However, suggested conservation measures include maintaining open-canopied forest stands as habitat for this species (Eltzroth, 2003). A major threat to Columbian white-tailed deer has been removal of “brush” during logging or agricultural development, which reduces the availability of both forage and cover (USFWS, 1983). For the western gray squirrel, forest practices that result in a reduction of mast-producing trees, particularly Oregon white oak (*Quercus garryana*), from stands dominated by large-diameter conifers is believed to reduce habitat quality (Linders and Stinson, 2006).

Breeding Bird Survey data from the Oregon, Washington, and the Southern Pacific Rainforest and Cascade Mountain physiographic strata, indicate declining population trends in one or more geographic category over the last two to four decades for 15 bird species associated with non-coniferous vegetation (Sauer et al., 2005; Table 1). Three species (Rufous hummingbirds, orange-crowned warblers, and MacGillivray’s warblers) had substantial evidence of population declines in three or more geographic categories. No trend was detected for 16 species, and 7 species had evidence of increasing populations in at least one geographic category.

4. Discussion

4.1. Functional bases of habitat relationships

The primary functional basis of the relationship of all species in Table 1 to non-coniferous vegetation was food resources, whether directly provided through vegetative material or mast, or indirectly through food webs. Herbivores, granivores, nectarivores, frugivores, and omnivores are directly associated with non-coniferous vegetation for food resources. These species rely on a wide diversity of grass, herb, shrub, and tree species to meet their energy needs year round or during critical periods (e.g., breeding season, winter). For example, fruits from deciduous trees and shrubs provide a critical resource for migrant birds, especially in the late summer and

Table 1

Species associated with non-coniferous vegetation in conifer forests of Oregon and Washington and the functional basis for the association (food or cover)

Common name	Scientific name	Food	Cover	Comments	References	Conservation status ^a
Reptiles and amphibians						
Del Norte Salamander	<i>Plethodon elongatus</i>	?		More abundant in stands with hardwoods than in pure conifer stands. Hardwood component likely influences food levels	Welsh and Lind (1995) and O'Neil et al. (2001)	OR: S(v); TNC: S3 (OR)
S. Alligator Lizard	<i>Elgaria multicarinata</i>	?	X	Herbaceous layer important for cover	O'Neil et al. (2001)	TNC: S5 (OR), S4? (WA)
Birds						
Bluebird, Western	<i>Sialia mexicana</i>	X		Diet includes fruits and berries; mistletoe is especially important winter food	Guinan et al. (2000) and Eltzroth (2003)	OR: S(v) TNC: S4 (OR), S3 (WA) BBS: no trend (OR, WA, SPR, CM)
Bushtit	<i>Psaltriparus minimus</i>	X	X	Associated with shrubby habitats	Sloane (2001)	TNC: S5 (OR), S4 (WA) BBS: decline (SPR), no trend (OR, WA, CM)
Chickadee, Black-capped	<i>Poecile atricapilla</i>	X	X	Mostly restricted to hardwood dominated habitats; diet includes seeds and fruits of shrubs and herbaceous plants	Smith (1993) and Strycker (2003)	TNC: S5 (OR, WA). no trend (OR, SPR, SPR, CM)
Finch, Purple	<i>Carpodacus purpureus</i>	X		Diet is primarily vegetative, including buds, fruits, seeds, and flowers of a wide variety of tree, shrub, and herbaceous species; typically nest in conifers	Vroman (2003b)	TNC: S4 (OR, WA). BBS: decline (SPR), no trend (OR, WA, CM)
Flycatcher, Dusky	<i>Empidonax oberholseri</i>	?	X	Associated with deciduous trees and shrubs in early seral habitats	Vroman (2003a)	TNC: S4 (OR, WA). BBS: decline (SPR), no trend (OR, WA, CM)
Flycatcher, Pacific-slope	<i>Empidonax difficilis</i>	?	X	Associated with deciduous canopy and sub-canopy trees in conifer-dominated forests; selection for red alder for nesting	Lowther (2000) and Leu (2000)	TNC: S4 (OR, WA). BBS: decline (OR, SPR), no trend (WA, CM)
Flycatcher, Willow	<i>Empidonax traillii</i>	?	X	Breeding habitat is dense deciduous thickets in riparian areas and early seral conifer forest; selects bracken fern (<i>Pteridium aquilinum</i>) for nesting	Altman (2003) and Mlodinow (2005a)	Fed: SoC; OR: S(v). TNC: S4 (OR, WA). BBS: decline (OR, SPR), no trend (WA, CM)
Grosbeak, Black-headed	<i>Pheucticus melanocephalus</i>	X	X	Occurs in conifer forests if deciduous vegetation present; diet consists of variety of insects and fruits	Trail (2003)	TNC: S5 (OR, WA). BBS: increase (WA, SPR, CM), no trend (OR)
Grosbeak, Evening	<i>Coccothraustes vespertinus</i>	X		Uses deciduous trees and shrubs for nesting and feeding; diet includes seeds, fruits, and buds of deciduous trees, including bigleaf maple and Cal. hazel (<i>Corylus nuttalli</i>)	Gillihan and Byers (2001) and Scheuering (2003b)	TNC: S5 (OR), S4 (WA). BBS: no trend (OR, WA, SPR, CM)
Grouse, Ruffed	<i>Bonasa umbellus</i>	X	X	Feeds on forbs, buds, catkins, and mast of understory shrubs and herbs, and arthropods; requires cover in understory for nesting; associated with alder stands in w. OR	Pelren (2003a) and Schroeder (2005)	TNC: S4 (OR), S5 (WA). BBS: no trend (OR, WA, SPR, CM)
Grouse, Sooty ^b	<i>Dendragapus fuliginosus</i>	X	X	Well-developed herb/grass/shrub stratum is a key component of breeding habitat for food and cover	Pelren (2003b)	TNC: S4 (OR, WA). BBS: no trend (OR, WA, SPR, CM)
Grouse, Spruce	<i>Falcapennis Canadensis</i>	X	X	Feeds on berries and foliage of shrubs and forbs in conifer dominated forests east of Cascade Mts.; <i>Vaccinium</i> especially important in summer; feeds exclusively on conifer needles in winter; adequate ground cover and shrubs may be important influence on nest success	Redmond et al. (1982) and Coggins (2003)	TNC: S3 (OR), S4 (WA). BBS: no data

Table 1 (Continued)

Common name	Scientific name	Food	Cover	Comments	References	Conservation status ^a
Hummingbird, Allen's	<i>Selasphorus sasin</i>	X	X	Feed and nest in willow (<i>Salix</i> spp.), blackberry (<i>Rubus</i> spp.), poison oak (<i>Toxicodendron diversilobum</i>), and other shrubs	Patterson and Scheuring (2003)	TNC: S3 (OR). BBS: no trend (SPR), no data (OR, WA, CM)
Hummingbird, Broad-tailed	<i>Selasphorus platycercus</i>	X	X	Feed on nectar of flowering shrubs and herbs; conifers, hardwoods, and herbs used for nesting	Calder and Calder (1992) and Scheuring and Patterson (2003b)	TNC: S2? (OR). BBS: no data
Hummingbird, Calliope	<i>Stellula calliope</i>	X		Feeds on nectar from flowering evergreen and deciduous shrubs in early seral habitat and forest openings; nests primarily in early shrub-sapling seral stage, usually on conifers; often on conifer cone	Calder and Calder (1994) and Scheuring and Patterson (2003a)	TNC: S4 (OR, WA). BBS: no trend (OR, WA, CM)
Hummingbird, Rufous	<i>Selasphorus rufus</i>	X	X	Feed and nest in open forests with well-developed understory; particularly associated with currant (<i>Ribes</i> spp.), salmonberry (<i>Rubus spectabilis</i>), Pacific madrone (<i>Arbutus menziesii</i>)	Patterson (2003)	TNC: S4 (OR, WA). BBS: decline (OR, WA, SPR); no trend (CM)
Junco, Dark-eyed	<i>Junco hyemalis</i>	X	X	Associated with early seral vegetation in forest openings; diet consists primarily of seeds of numerous plant species	Nehls (2003b)	TNC: S5 (OR, WA). BBS: no trend (OR, WA, SPR, CM)
Pigeon, Band-tailed	<i>Patagioenas fasciata</i>	X		Feeds on mast and fruit of hardwood trees and shrubs; nests primarily in conifers	Sanders and Jarvis (2003) and Wahl (2005)	TNC: S3 (OR, WA). BBS: no trend (OR, WA, SPR, CM)
Quail, Mountain	<i>Oreortyx pictus</i>	X	X	Strongly associated with shrubs in early seral forests for food and cover; consume foliage, berries, and insects from wide variety of shrub and herbaceous species	Pope (2003) and Schirato (2005)	OR: U; TNC: S4 (OR), S1 (WA). BBS: increase (SPR), no trend (OR, WA, CM)
Solitaire, Townsend's	<i>Myadestes townsendi</i>	X		Fruit from shrubs, including huckleberry, salal, and blackberry, important in diet during non-breeding season	Dowlan (2003a)	TNC: S4 (OR, WA). BBS: increase (OR), No trend (WA, SPR, CM)
Sparrow, Fox	<i>Passerella iliaca</i>	X	X	Strongly associated with dense shrub growth; diet includes fruits and seeds from mast-producing vegetation	Weckstein et al. (2002) and Contreras (2003)	TNC: S4 (OR, WA). BBS: decline (OR, CM), no trend (WA, SPR)
Sparrow, White-crowned	<i>Zonotrichia leucophrys</i>	X	X	Associated with shrubby openings and clearcuts in forested landscapes; seeds, buds, grass, and fruits important in diet	Herlyn (2003)	TNC: S5 (OR, WA). BBS: decline (OR, SPR), no trend (WA, CM)
Thrush, Hermit	<i>Catharus guttatus</i>	X		Fruits and berries of mast-producing shrubs important in diet, especially during migration and winter; frequently nests in conifers	Nehls (2003a)	TNC: S4 (OR, WA). BBS: decline (OR), no trend (WA, SPR, CM)
Thrush, Swainson's	<i>Catharus ustulatus</i>	X	X	Associated with deciduous mid- and understory in closed canopy conifer forests; consumes fruit from mast-producing shrubs	Hagar (2003a)	TNC: S5 (OR), (WA). BBS: decline (OR, SPR), no trend (WA, CM)
Thrush, Varied	<i>Ixoreus naevius</i>	X		Fruit from mast-producing shrubs important in diet, especially post-breeding; frequently nests in conifers. Breeding varied thrushes reach highest abundance in late-seral conifer forests in Pacific Northwest	George (2000) and Hagar (2003b)	TNC: S4 (OR), S5 (WA). BBS: no trend (OR, WA, SPR, CM)
Veery	<i>Catharus fuscescens</i>	X	X	Forages and nests in dense understory shrubs and riparian thickets; diet is primarily insectivorous, also eats fruit	Fish and Contreras (2003) and Buchanan (2005)	TNC: S4 (OR), S3 (WA). BBS: no trend (OR, WA, CM)
Vireo, Cassin's	<i>Vireo cassinii</i>	?	X	Associated with deciduous habitats	Goguen and Curson (2002)	TNC: S4 (OR, WA). BBS: no trend (OR, WA, SPR, CM)

Vireo, Hutton's	<i>Vireo huttoni</i>	?		Associated with closed canopy, mixed conifer-hardwood forest, with deciduous mid- and understory. Also abundant in evergreen oak and madrone habitats; commonly nests in Douglas-fir (<i>Pseudotsuga menziesii</i>)	Scheuring (2003a) and Grettenberger (2005)	TNC: S4 (OR), S5 (WA). BBS: increase (OR), no trend (WA, SPR, CM)
Vireo, Red-eyed	<i>Vireo olivaceus</i>	X	X	Associated with deciduous habitats including cottonwood, bigleaf maple, red alder, ash, and willow	Korpi (2003) and Mlodinow (2005b)	TNC: S4 (OR), S3 (WA). BBS: decline (WA), no trend (OR, SPR, CM)
Vireo, Warbling	<i>Vireo gilvus</i>	X	X	Strongly associated with deciduous trees, including red alder, bigleaf maple, ash (<i>Fraxinus</i> spp.) and cottonwood (<i>Populus</i> spp.). Occurs in conifer forest only where deciduous trees present	Gardali and Ballard (2000) and Heltzel (2003)	TNC: S5 (OR, WA). BBS: increase (WA, CM), no trend (OR, SPR)
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	?	?	Associated with deciduous component of conifer forests	Guzy and Lowther (1997) and Chappell (2005)	TNC: S5 (OR, WA). BBS: no trend (OR, WA, SPR, CM)
Warbler, MacGillivray's	<i>Oporornis tolmiei</i>	X	X	Associated with shrubs and deciduous vegetation in conifer forests; primarily forage in low shrubs and herbs	Dowlan (2003b)	TNC: S4 (OR, WA). BBS: decline (OR, WA, SPR, CM)
Warbler, Nashville	<i>Vermivora ruficapilla</i>	X	X	Feed and breed in shrubby, early seral habitat; insectivorous	Janes (2003)	TNC: S4 (OR, WA). BBS: no trend (OR, WA, SPR, CM)
Warbler, Orange-crowned	<i>Vermivora celata</i>	X	X	Forage for arthropods on deciduous trees and shrubs; frequently conceals nests under herbaceous or shrub cover, or in or under ferns	Sogge et al. (1994) and Dillingham (2003)	TNC: S5 (OR), S4 (WA). BBS: decline (OR, WA, SPR), no trend (CM)
Warbler, Wilson's	<i>Wilsonia pusilla</i>	X	X	Strongly associated with tall deciduous shrubs in forest understory; frequently nests in swordfern (<i>Polystichum munitum</i>)	Hagar (2003c)	TNC: S5 (OR, WA). BBS: decline (WA, SPR), no trend (OR, CM)
Woodpecker, Downy	<i>Picoides pubescens</i>	X	X	Forages primarily on deciduous trees and shrubs (insects and mast); majority of nests in conifer forests are in deciduous trees	Jackson and Ouellet (2002) and Simmons (2003)	TNC: S4 (OR, WA). BBS: no trend (OR, WA, SPR, CM)
Wood-pewee, Western	<i>Contopus sordidulus</i>	?	X	Associated with deciduous trees, especially Oregon white oak	Schrock (2003)	TNC: S4 (OR), S5 (WA). BBS: decline (OR), increase (WA), no trend (SPR, CM)
Wren, Bewick's	<i>Thryomanes bewickii</i>	?	X	Nests and forages in shrubby thickets; primarily insectivorous	Peck (2003)	TNC: S4 (OR), S5 (WA). BBS: increase (WA), no trend (OR, SPR, CM)
Wrentit	<i>Chamaea fasciata</i>	X	X	Feed and breed in dense, shrubby understory; eats fruit and seeds in addition to arthropods	Geupel and Ballard (2002)	TNC: S5 (OR, WA). BBS: no trend (OR, SPR)
Mammals Bat spp.	<i>Chiroptera</i>	?		In general, positive relationships between levels of bat activity and amount of deciduous vegetation in riparian areas, probably an indirect influence of insect prey associated with deciduous trees	Ober and Hayes (2005)	
Bat, Hoary	<i>Lasiurus cinereus</i>	?	?	May use deciduous trees for roosting in PNW conifer forests; may be indirectly associated with deciduous vegetation through lepidopteran prey	Whitaker et al. (1977), J.P. Hayes, personal communication and O'Neil et al. (2001)	TNC: S3 (OR, WA)
Bat, Townsend's Big-eared	<i>Corynorhinus townsendii</i>	?		Diet is 95% moths; may be indirectly associated with deciduous vegetation through lepidopteran prey	Whitaker et al. (1977)	Fed.: SoC; OR: S(c); WA: SC. TNC: S2 (OR, WA)
Bear, Black	<i>Ursus americanus</i>	X		Mast from shrubs and hardwood trees is important food	Verts and Carraway (1998)	TNC: S4 (OR), S5 (WA)
Chipmunk, Allen's	<i>Neotamias senex</i>	X		Flowers and seeds of herbs and shrubs important in diet	Gannon and Forbes (1995)	TNC: S4 (OR)

Table 1 (Continued)

Common name	Scientific name	Food	Cover	Comments	References	Conservation status ^a
Chipmunk, Red-tailed	<i>Neotamias ruficaudus</i>			Eats seeds and fruits of variety of understory plants	Best (1993) and O'Neil et al. (2001)	TNC: S2 (WA)
Chipmunk, Siskiyou	<i>Neotamias siskiyou</i>	X		Extensive use of mast produced by non-coniferous vegetation	O'Neil et al. (2001)	TNC: S4 (OR)
Chipmunk, Townsend's	<i>Neotamias townsendii</i>	X		Mycophagous, but also consume seeds of woody plants; associated with well-developed understories that include variety of fruit- and seed-producing shrubs and trees	Doyle (1990) and Carey (1995)	TNC: S4 (OR), S5 (WA)
Chipmunk, Yellow-pine	<i>Neotamias amoenus</i>	X		Seeds of grasses and pines, and fruits of understory plants important in diet	Sutton (1992) and O'Neil et al. (2001)	TNC: S4 (OR), S5 (WA)
Deer, Black-tailed	<i>Odocoileus hemionus</i>	X		Primarily browsers. Shrubs, especially <i>Rubus</i> spp., and forbs provide important browse; also eat mast of fruit- and nut- producing spp.	Maser et al. (1981) and Verts and Carraway (1998)	TNC: S5 (OR, WA)
Deer, Columbian White-tailed	<i>O. virginianus leucurus</i>	X		Feed on herbs, forbs, mast	Verts and Carraway (1998)	Fed.: E; OR: S(v); WA: E. TNC: S2 (OR), S1 (WA)
Deermouse	<i>Peromyscus maniculatus</i>	X		Forest sub-species eats seeds, nuts, and fruits produced in forest understory	Carey and Johnson (1995) and Carey and Harrington (2001)	TNC: S5 (OR, WA)
Deermouse, Northwestern	<i>Peromyscus keeni</i>	X		Associated with dense shrubs in old-growth western hemlock forest; positive association with vine maple, the large seeds of which provide high-quality food	Carey and Harrington (2001)	TNC: S4 (WA)
Elk	<i>Cervus elaphus</i>	X		Primarily grazers. Grass, forbs, and shrubs in early seral forests provide important forage	Maser et al. (1981) and Witmer et al. (1985)	TNC: S5 (OR, WA)
Gopher, W. Pocket	<i>Thomomys mazama</i>	X		Eats wide variety of grasses and forbs	Verts and Carraway (2000)	TNC: SNR (OR), S2 (WA)
Ground Squirrel, Cascade Golden-mantled	<i>Spermophilus lateralis</i>	X		Feeds on understory mast in pine forests; fungi (especially in fall), green vegetation, seeds, and small fruits, are included in diet	Trombulak (1988) and O'Neil et al. (2001)	TNC: S4 (OR), S5 (WA)
Hare, Snowshoe	<i>Lepus americanus</i>	X	X	Browse on wide variety of herbaceous plants and shrubs in understory of conifer forest	Maser et al. (1981) and Koehler (1990)	TNC: S4 (OR), S5 (WA)
Mole, Shrew	<i>Neurotrichus gibbsii</i>	X	?	Inhabits soil under hardwoods, especially bigleaf maple and red alder; lichen important in diet seasonally	Maser et al. (1981), Gomez (1992) and Carey and Harrington (2001)	TNC: S4 (OR), S5 (WA)
Moose	<i>Alces americanus</i>	X		Early seral shrubs and forbs provide important browse, especially willow spp.	Franzmann (1981)	TNC: S2 (WA)
Mountain Beaver	<i>Aplodontia rufa</i>	X		In Coast Range, diet consists mainly of bracken and sword ferns	Maser et al. (1981)	TNC: S4 (OR), S5 (WA)
Mouse, Pacific Jumping	<i>Zapus trinotatus</i>	X		PNW endemic; associated with herbs and shrubs where occurs in forested habitats	Doyle (1990), Gomez (1992) and Martin and McComb (2002)	TNC: S4 (OR), S5 (WA)
Porcupine, Common	<i>Erethizon dorsatum</i>	X		Feeds seasonally on non-coniferous vegetation in coniferous forests. Reaches highest abundance in mixed coniferous and hardwood forests	O'Neil et al. (2001)	TNC: S5 (OR, WA)
Ringtail	<i>Bassariscus astutus</i>	X		Omnivorous; includes mast, plant material, and nectar in diet	Poglayen-Neuwall and Towell (1988)	OR: U. TNC: S3 (OR)
Shrew, Baird's	<i>Sorex bairdi</i>	?	?	Positive association with herbaceous and shrub layer of forests; Endemic to Oregon	O'Neil et al. (2001)	TNC: SU (OR)
Shrew, Montane	<i>Sorex monticolus</i>	?	?	Associated with ericaceous shrubs; often listed as "early seral" but occurs throughout forest sere as long as suitable understory components present	Carey and Harrington (2001)	TNC: S4 (OR, WA)
Shrew, Pacific	<i>Sorex pacificus</i>	?	?	Favors red alder stands with high deciduous shrub cover; Endemic to western Oregon	Maser et al. (1981), Gomez (1992) and Martin and McComb (2002)	TNC: S3 (OR)
Shrew, Trowbridge's	<i>Sorex trowbridgii</i>	?	?	Positive association with tall deciduous shrubs	Carey and Johnson (1995)	TNC: S4 (OR), S5 (WA)

Shrew, Vagrant	<i>Sorex vagrans</i>	?	?	Positively associated with herbaceous cover and red alder	Carey and Harrington (2001) and Martin and McComb (2002)	TNC: S4 (OR), S5 (WA)
Squirrel, Douglas'	<i>Tamiasciurus douglasii</i>	X		Seeds of woody plants and fungus important in diet; Cal. Hazel important in times of cone shortages; positively associated with ericaceous shrubs	Carey (1995) and O'Neil et al. (2001)	TNC: S5 (OR, WA)
Squirrel, Northern Flying	<i>Glaucomys sabrinus</i>	X	X	Primarily mycophagous, but also positively associated with ericaceous shrubs; Uses lichens as food and nesting material	Carey (1995) and O'Neil et al. (2001)	TNC: S4 (OR, WA)
Squirrel, W. Gray	<i>Sciurus griseus</i>	X	X	Strongly associated with OR white oak for food (acorns) and cavities, especially in WA	Carraway and Verts (1994)	OR: U; WA: T. TNC: S4 (OR), S2 (WA)
Vole, Creeping	<i>Microtus oregoni</i>	X		Abundant in early seral habitats with high herbaceous cover; eats forbs and grasses	Doyle (1990) and Carey and Johnson (1995)	TNC: S4 (OR, WA)
Vole, Heather	<i>Phenacomys intermedius</i>	X		Feeds on bark and buds of shrubs and heaths in winter, and primarily on green vegetation, berries, and seeds in summer	McAllister and Hoffman (1988)	TNC: S4 (OR), S5 (WA)
Vole, Long-tailed	<i>Microtus longicaudus</i>	X		Positive association with deciduous shrubs; berries important food for juveniles, forbs necessary component of winter diet	Van Horne (1982) and Gomez (1992)	TNC: S5 (OR, WA)
Vole, S. Red-backed	<i>Myodes gapperi</i>	X		Positive association with understory development; eats fungus, lichens, seed of woody plants	Carey and Johnson (1995)	TNC: S4 (OR), S5 (WA)
Vole, W. Red-backed	<i>M. californicus</i>	X		Positive association with cover of broad-leaved evergreen shrubs	Doyle (1990) and Gomez (1992)	TNC: S4 (OR)
Vole, White-footed	<i>Arborimus albipes</i>	X		Forages on shrubs and other understory vegetation; especially associated with red alder and Cal. hazel	Voth et al. (1983), Gomez (1992) and Manning et al. (2003)	Fed: SoC; OR: U. TNC: S3 (OR)
Woodrat, Dusky-footed	<i>Neotoma fuscipes</i>	X		Diet includes leaves, fruits, and flowers from a wide range of vegetation; also eats ferns	Maser et al. (1981) and Carraway and Verts (1991)	TNC: S4 (OR)

Blank cells indicate that no evidence was found for functional association; “?” indicates unclear or potential indirect functional relationship. Species are listed alphabetically by common name within taxonomic class(es).

^a Federal conservation status (Fed.): E = endangered; SoC = species of concern; State status OR – designated by Oregon Department of Fish and Wildlife (ODFW 1997): S(c) = sensitive (critical); S(v) = sensitive (vulnerable); U = undetermined; State status WA – designated by Washington Department of Fish and Wildlife: E = endangered SC = State Candidate; T = threatened. TNC Rank at State scale: 1 = critically imperiled; 2 = imperiled; 3 = vulnerable to extirpation or extinction; 4 = apparently secure; 5 = demonstrably widespread, abundant, and secure; SU = unrankable due to lack of information; SNR = currently unranked. For birds, population trend is from BBS data for Oregon (OR), Washington (WA), and South Pacific Rainforest (SPR), and Cascade Mountains (CM) physiographic regions: decline = significant short term (since 1980) or long term (since 1966) decrease; increase = significant short term (since 1980) or long term (since 1966) increase; no trend = no evidence of change; no data = species not adequately detected by BBS.

^b Formerly Blue Grouse (*Dendragapus obscurus*).

fall (Parrish, 1997), and for mammals such as squirrels, chipmunks, bear, and ringtail (Martin et al., 1961). Many species of rodents (e.g., chipmunks), and resident birds (e.g., chickadees, nuthatches, jays) cache seeds and nuts from a diversity of plant species in order to meet energy requirements throughout the winter (Maser et al., 1981; Erlich et al., 1988). Even species that are primarily insectivorous, such as shrew mole, Trowbridge's shrew, and montane shrew, also eat seeds of non-coniferous species (e.g., salal (*Gaultheria shallon*) and huckleberry (*Vaccinium* spp.); Carey and Harrington, 2001). Many species that rely directly on vegetation and mast for food are associated with early successional vegetation in forest gaps or regenerating stands. The light-rich environment of gaps results in greater production of flowers and fruits than the shaded matrix (Harrington et al., 2002).

The majority of species that were indirectly associated with non-coniferous vegetation (“?” in Table 1) were primarily insectivorous, including passerines such as flycatchers, vireos, and warblers, and mammals such as shrews and bats. Insectivores may be linked to certain plant taxa through their insect prey (Holmes and Robinson, 1981) because most forest insects use specific host plant species (Edwards and Wratten, 1980), and diversity and abundance of herbivorous insects varies among plant species (Schowalter, 2000). Important differences in arthropod communities among deciduous trees and shrubs, herbaceous vegetation, and conifers likely underlie the association of many insectivorous species with non-coniferous vegetation. In particular, Lepidoptera, which are important prey for many insectivores, are more diverse and abundant on hardwood trees and shrubs than on conifers in Pacific Northwest conifer forests (Hammond and Miller, 1998). In coniferous forests in western Oregon, hardwoods supported 57% of the lepidopteran species richness and 69% of their abundance (Hammond and Miller, 1998). Studies of herbivory indicate that lepidopteran herbivores are uncommon on mature conifers (Schowalter and Ganio, 1998) and contrastingly abundant on broad-leaved vegetation in the understory (Shaw et al., 2006). Herbs and grasses also support a significant proportion of Lepidoptera species in western Oregon (31%; Hammond and Miller, 1998) and have been positively associated with arthropod abundance in general (Blenden et al., 1986). In addition to providing prey for a diverse vertebrate fauna, the rich arthropod communities supported by non-coniferous vegetation make a significant contribution to biodiversity in their own right, by performing diverse and critically important roles in ecosystem functioning (Kim, 1993).

Further evidence for the role of arthropod prey in mediating associations between particular types of vegetation and insectivores comes from the observation that many neotropical migrant bird species that rely heavily on lepidopteran larvae as a food resource during the breeding season in temperate forests (Holmes et al., 1979; Graber and Graber, 1983; Sample et al., 1993) also are associated with deciduous trees and shrubs (Morrison and Meslow, 1983; Willson and Comet, 1996b). Similarly, the observed affinity of bats for areas dominated by deciduous vegetation may be related to the importance of adult

Lepidoptera as prey for several species of bats in Pacific Northwest forests (Whitaker et al., 1977; Ober and Hayes, 2005). Although such correlative relationships have been established for many insectivorous species (see references in Table 1), empirical links between the availability of preferred arthropod prey and vegetation species or type have rarely been made. In one of the few studies to illustrate a functional link between an insectivore and habitat, Hagar (2004) showed that tall, deciduous shrubs supported high abundances of arthropod taxa selected as prey by Wilson's warblers.

Some species that may be indirectly associated with non-coniferous vegetation may have been excluded from the list due to lack of evidence for a relationship between abundance and vegetation composition, or incomplete knowledge. For example, there is little evidence for strong associations between non-coniferous vegetation and most upper-level consumers in forest food webs. However, mammalian predators and raptors may indirectly rely on non-coniferous vegetation that supports their prey. For example, lynx (*Lynx canadensis*) are indirectly linked to forage for snowshoe hare through a close predator-prey relationship (Koehler, 1990). Similarly, 90% of the diet of northern spotted owls (*Strix occidentalis*) is composed of small mammals that are associated with non-coniferous vegetation, including northern flying squirrels, wood rats, and other rodents (Forsman et al., 1984; Table 1). Ward et al. (1998) found that northern spotted owls in northwestern California selected hardwood-conifer edges where their primary prey, the dusky-footed wood rat, was most abundant. The highest densities of wood rats in their study were associated with stands of dense shrubs and sapling hardwoods. Glenn et al. (2004) also found a positive relationship between northern spotted owls and the amount of broad-leaved forest in western Oregon. They suggested that the presence of broad-leaved habitats in young forests may allow spotted owls to survive in landscapes with less late-seral forest than typically characterizes suitable habitat because of the positive influence on prey abundance.

Indirect relationships also may underlie positive associations between abundance of herpetofauna and deciduous vegetation (Gomez and Anthony, 1996), although amphibians and reptiles are not well represented in Table 1. Habitat for amphibians and reptiles is often best described by conditions on the forest floor, such as substrate characteristics and amounts of decaying wood (Bury et al., 1991), with little evidence for functional associations of amphibians and reptiles with any kind of vegetation (R.B. Bury, personal communication). However, microclimate and soil properties may differ beneath hardwoods compared to conifers, providing different cover and food resources for wildlife that dwell on the forest floor. In particular, leaf litter has an important influence on the abundance and composition of soil arthropods (Bultman and Uetz, 1984). Differences in leaf chemistry and decay rate between deciduous hardwoods and conifers may influence soil food webs through litter effects on arthropods (Koivula et al., 1999; Matkins, 2005). For example, a higher concentration of available soil nitrogen in alder – than in conifer-dominated riparian stands in the Pacific Northwest (Gregory et al., 1991)

might be expected to scale up through arthropod prey into salamander abundance (de Maynadier and Hunter, 1995). These processes also may explain why five species of shrew and the shrew mole are associated with understory and deciduous components of conifer forests (Table 1). Soil invertebrates are important in the diets of all of these species. Additionally, arthropod prey availability on the forest floor may be influenced by vegetation composition through variation in diversity and abundance of arthropods that fall from different plant species (Southwood, 1961). Allocthonous inputs of arthropods into stream systems can vary with canopy tree species, influencing prey availability for salmonids and aquatic amphibians (Wipfli, 1997; Romero et al., 2005), and other consumers in aquatic food webs, such as American dipper (*Cinclus mexicanus*) and harlequin duck (*Histrionicus histrionicus*). Similar processes might be expected to influence arthropod prey availability on the forest floor in terrestrial systems. In support of this, Willson and Comet (1996a) found more invertebrates in the leaf litter and live foliage of deciduous stands than conifer stands, paralleling patterns of higher abundance and diversity of birds.

4.2. Management considerations

Recent concern over biodiversity in managed forests has focused on mid-seral stands, where dense conifer canopies have excluded understory vegetation, creating stands of homogeneous structure that support low diversity of wildlife (Hayes et al., 1997). Partial harvests such as thinning and group selection are among the practices being developed to increase structural and compositional diversity in young managed forests (McComb et al., 1993; Chambers et al., 1999; Carey et al., 1999). By reducing canopy cover and increasing light availability to the understory, thinning can promote the development of vegetation near the forest floor (Kerns et al., 2003). Evidence is accumulating for the potential of commercial thinning in second-growth conifer stands to increase bird and mammal diversity (Hagar et al., 1996, 2004; Haveri and Carey, 2000; Carey and Wilson, 2001). Alternatives to clear-cut regeneration systems, or uneven-aged management, may offer options for maintaining habitat for understory species in older stands (McComb et al., 1993). Group selection involves the removal of small clusters of mature trees to create a mosaic of even-aged patches within a stand, and may mimic natural disturbances such as root-rot pockets (Chambers et al., 1999). Early seral conditions in recently harvested patches approach those in a clear-cut as patch size increases (Curtis et al., 1998), potentially providing habitat for some shrub-associated species (Chambers et al., 1999).

Although partial harvests have shown some promise for enhancing diversity in mid-seral forests, their ability to provide adequate understory resources for the entire suite of associated biodiversity is limited. In the first place, the mechanical process of harvesting may damage tall shrubs, resulting in a short-term decrease of shrub cover (Curtis et al., 1998) and a corresponding decrease in habitat suitability for species associated with shrubs. In addition, shrubs may be slow to

respond to canopy reduction after long periods of suppression under dense overstory (Hanley, 2005). Differences in abundance of understory plants between thinned and unthinned stands in the Coast Range may take more than a decade to emerge (Alaback and Herman, 1988). Not only does it take time for shrubs to respond vegetatively to thinning, but mast production is also delayed because larger, older shrubs are more likely to flower and produce seeds than smaller, younger shrubs (Harrington et al., 2002). Prescriptions for thinning may be most effective at enhancing diversity if they explicitly address goals for understory vegetation structure and composition as well as the traditional attention to overstory characteristics.

Controlling density at an early age, before canopy closure, can help to maintain diverse stand structure throughout the life of a stand, and can preserve future management options (Tapeiner et al., 2002). According to models of succession in forests that develop naturally following disturbance, wide spacing and delayed dominance of conifers in naturally regenerating stands (Tapeiner et al., 1997) would maintain a vigorous understory throughout much of stand development. It is not surprising then that many wildlife species that are said to be associated with early seral habitat can occur with great regularity and in abundance throughout all stages of forest development as long as the necessary habitat elements are present. For example, although montane shrews, creeping voles, and deer mice are often listed as early seral species, Carey and Johnson (1995) found these species in both young and old forests where their occurrence was more correlated with cover of understory vegetation and woody debris than forest age. Similarly, in a chronosequence of unmanaged forest stands throughout Oregon and Washington, understory characteristics had low discriminatory power for age classes (Spies and Franklin, 1991), and most vertebrate wildlife species associated with understory vegetation did not differ in abundance among forest age classes (Ruggiero et al., 1991: 456–462). This suggests that the maintenance of adequate understory throughout forest development would be a good strategy for enhancing biodiversity in managed forest stands.

Finally, vegetation management that accelerates establishment and dominance of conifers following harvest or stand-replacing natural disturbances has contributed to the reduction of shrub and hardwood tree cover in some conifer-dominated regions (Kennedy and Spies, 2004). A decrease in the duration of shrub cover in early seral stands also limits the temporal availability of this diverse stage of forest development (Lautenschlager, 1993). In managed forest landscapes where enhancing biodiversity is a goal, the practice of controlling broad-leaved vegetation in clearcuts and after fires should be carefully re-evaluated. Early seral stands dominated by shrubs or deciduous trees (e.g., red alder) represent opportunities to foster biodiversity on a landscape scale.

5. Conclusions

The presence of herbs, and broad-leaved shrubs and trees has an important influence on food and cover resources for wildlife in Pacific Northwest conifer forests. In particular,

non-coniferous vegetation provides the foundation for food webs that contribute to diversity at multiple trophic levels, ultimately influencing the abundance and distribution of vertebrate consumers. Furthermore, the array of food resources provided by a diverse community of understory vegetation likely confers overall resource stability, even for species that primarily or seasonally depend on conifers as a food source. Because broad-leaved shrubs and trees in conifer-dominated forests function in a fundamentally different way than understory conifer seedlings and saplings, they add both structural and functional diversity to forest stands. Thus, planting conifers in the understory as a means of increasing structural diversity will likely have a limited impact on functional diversity. In contrast, encouraging development of a variety of herbs, shrubs, and broad-leaved trees in the mid-story and understory is likely to increase both structural and functional diversity within a forest stand.

Wildlife species that depend on the resources provided by non-coniferous vegetation may not persist in forests where these components are scarce. Although the degree of dependence on non-coniferous vegetation is not well understood for most species, the number of associated species implies that the maintenance of a diverse plant community will be an important strategy for fostering biodiversity in managed conifer forests. It is important to recognize that the number of species influenced by non-coniferous vegetation likely extends beyond those listed in Table 1 to include upper-level consumers such as mammalian predators, raptors, and herpetofauna. Although documentation of strong, direct associations is scarce, an important indirect link to non-coniferous vegetation clearly exists for many species in these groups through their vertebrate or invertebrate prey. Perhaps of greatest immediate concern to managers, management activities that influence the development of non-coniferous vegetation have the potential to impact habitat for special-status species and species with declining population trends. Management practices that affect deciduous trees and shrubs may have the most important consequences for special-status species that are commonly associated with these elements in forested habitats, such as white-footed voles and Townsend's big-eared bats. Forest practices are less likely to significantly impact populations of species that also use non-forested habitats, such as willow flycatcher and western bluebird. For several species, such as Del Norte Salamander and ringtail, a lack of information on habitat relations makes it difficult to assess potential responses to management. Providing habitat for a diverse native fauna will entail explicit recognition of non-coniferous habitat elements in management plans and strategies. This will require a departure from past practices that were either indifferent to non-coniferous vegetation, or were aimed at reducing competition with commercially valuable conifers.

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