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Biological associates of early-seral pre-forest in the Pacific Northwest

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ABSTRACT

Traditionally overlooked by foresters as unproductive and ecologists as disorganized, naturally regenerating forests in the Pacific Northwest (PNW) are perhaps the least understood forest condition in the region. More recently, concerns over the rarity of this forest condition have sparked interest in identifying ecological characteristics unique to forested sites after a canopy-opening disturbance and before the re-establishment of a closed conifer canopy. Here we review the literature to identify the plant and animal associates of early-seral pre-forests in the PNW in order to provide baseline information pertaining to the recognition and conservation role of early-seral pre-forest ecosystems. We describe a number of bird, mammal, insect, amphibian and reptile species associated with PNW early-seral pre-forests either by empirical observation or inferred through life-history characteristics in an attempt to formally identify unique species indicators of naturally regenerating pre-forest communities. For Washington, Oregon, and northern California, we also review the state lists of endangered, threatened, monitored or otherwise conservation-listed species (664 unique species or subspecies for the combined region) to assess the proportion of protected species that rely on the structural attributes of early-seral pre-forests. Here, we found that these proportions are comparable to the proportions reliant on mature or late-seral forest. In addition, greater than 50% of all listed species for each of the three regions were partial or facultative users of early-seral pre-forest ecosystems. This assessment suggests that naturally structured early-seral pre-forests in the PNW provide key habitat for many species, including obligates and near-obligates, and that future research should seek to refine our understanding of the specific structural and compositional attributes that form the basis of these associations.

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1. Introduction

Naturally regenerating post-disturbance (early-seral) communities are increasingly recognized for their relevance to forest management, especially in landscapes where conservation of organisms, provision of habitat, non-timber forest products, and other ecosystem values are included in management objectives (Gobster, 2001; Swanson et al., 2011). In the Pacific Northwest (PNW) of the United States, ecosystem management on federal forest land is beginning to evolve from its recent emphasis on old-growth conservation toward managing for all characteristic seral stages, ranging from old-growth to structurally diverse early-seral (or pre-forest) communities (Franklin and Johnson, 2012). Defined as the successional stage occurring between a stand-replacing disturbance (including wildfire, wind, volcanic eruption, severe flood, and snow avalanche) and subsequent tree canopy closure

(Swanson et al., 2011), naturally regenerating early-seral pre-forest communities are unique in being co-dominated by a wide range of plant forms including grasses, herbs, broadleaf shrubs, and hardwood and coniferous trees, and accompanied by the living and dead woody legacies of the pre-disturbance stand. These plant communities have been associated with a similarly diverse set of vertebrate and invertebrate animal taxa (Hammond and Miller, 1998; Hagar, 2007; Betts et al., 2010) and are often posited as the most species-diverse stage of forest succession (e.g., Franklin and Spies, 1991).

The knowledge base on naturally generated early-seral pre-forest in PNW forests, including structural attributes, is surprisingly sparse, owing in part to their rarity on the landscape relative to historic levels. The percentage of the regional landscapes of the PNW in early succession was historically highly variable in space and time, but reconstructions (Teensma et al., 1991 for the Oregon Coast Range, Takaoka and Swanson, 2008 for the Oregon Cascades) demonstrate a $\geq 50\%$ reduction in the proportion of the landscape in a pre-canopy closure condition when comparing the 19th and

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early 20th centuries to the present. The proportion of naturally disturbed area has similarly declined in the conifer forests of the Northern Rockies (Gruell, 1980; Brown et al., 1994; Hutto, 1995). Based on the observed fire regime, Wimberly et al. (2000) concluded that late seral forest in the Oregon Coast Range fluctuated between 25% and 75% of the landscape at the province scale. It is reasonable to expect that much of the balance would have been in a true pre-crown closure condition rather than young stem-exclusion forests, considering the protracted rates of recovery to a closed-canopy condition in landscapes historically (Tappeiner et al., 1997; Poage et al., 2009; Freund et al., 2014). When the focus is further restricted to structurally complex early-seral pre-forest conditions, such as those generated by natural disturbance and with abundant biological legacies, the proportion of the modern landscape in such a condition is even more likely lower than in the past. As in many commodity-producing forest regions, harvest-created younger age classes are currently well represented in the PNW (e.g., Ripple et al., 2000), but widespread management practices have emphasized dense, homogeneous conifer establishment and rapid canopy closure in young stands (e.g., Oregon Forest Practices Rules, 2013), effectively truncating or skipping the early-seral pre-forest stage. This approach is highly proven in terms of efficient fiber production, but has greatly reduced the abundance of the early-seral pre-forest stage relative to pre-settlement ranges (e.g., Kennedy and Spies, 2004). Accordingly, relatively little attention has been paid by either the scientific or management community to the composition, structure, or function of natural early-seral pre-forest forests in the PNW. However, with intensified disturbance rates in recent years (e.g., wildfires), consideration of the early-seral condition is increasing in this region as well as several others (Schlossberg et al., 2010; Swanson et al., 2011; Donato et al., 2012; *Articles in this issue*).

A key limitation in our understanding of natural early-seral pre-forests is to what degree they are associated with, or even indicated by, particular flora and fauna. In the case of vegetation, which fundamentally structures forest ecosystems, certain species may serve to both indicate and define natural early-seral pre-forest communities. Indicator species are widely used for distinguishing habitat types in space, such as edapho-climatic environments (Klinka et al., 1989), but they can also be used to distinguish temporal changes in system conditions over a forest sere. For example, in the PNW, late-successional old-growth forests are closely associated with, among other things, certain lichen species (Peterson and McCune, 2001), the conifer Pacific yew (*Taxus brevifolia*) (Busing et al., 1995), and the northern spotted owl (*Strix occidentalis caurina*) (Davis et al., 2011). Yet this has scarcely been explored for younger, post-disturbance age classes. Hagar (2007) provided a very relevant review, focused on vertebrate wildlife and describing associations of dozens of birds, mammals, and herpetofauna with broadleaf vegetation that typically characterizes open, early-seral pre-forest conditions, and we attempt to build upon this work by examining a range of other structural and compositional attributes.

In this paper, we review literature and other data sources to identify plant and animal affinity toward specified attributes of early-seral pre-forests in the PNW. Our specific objectives are:

1. Identify key structural attributes that distinguish *archetypal* early-seral pre-forest from other forest and non-forest ecosystems in the PNW.
2. Present examples of plant and animal species with affinities toward the structural attributes of early-seral pre-forest.
3. Compare the number of threatened or endangered species associated with, or dependent on, the structural attributes of early-seral pre-forest, to the number of threatened or endangered species associated with or dependent on the structural attributes of old-growth forest.

The geographic scope of this study is the PNW of the United States, here defined as the maritime temperate zone from northern California to Washington State, and extending inland to western Montana. The diverse forest types in this region are generally dominated by long-lived conifer trees and many experience some form of stand-replacing disturbance on various time scales (Schmidt et al., 2002) – either as large high-severity fires over long time intervals or smaller patches of stand-replacing fire within a mixed-severity context, severe windstorms, or severe insect outbreaks (Franklin and Dyrness, 1988; Agee, 1993). Many of the attributes of early-seral pre-forest explored here are not strictly limited to landscapes with low-frequency, stand-replacing events, but are also of importance at various spatial scales in landscapes with mixed-severity disturbance regimes (Hessburg et al., 2007; Halofsky et al., 2011; Perry et al., 2011). We generally excluded studies pertaining to the central and southern Rocky Mountains, interior northern Canada, and southern and interior California; however, a few such references are noted when they contain broadly applicable relevance.

2. Structural attributes of early-seral pre-forest in the PNW

Just as identifying the structural attributes of old-growth depends to some degree on operational definitions, identifying the structural attributes of early-seral pre-forests is afforded by first defining an archetype relative to other forest conditions. For the purposes of this paper, we define the *archetypal* early-seral pre-forest in the PNW as an ecosystem in the early stages of secondary succession following a natural canopy-killing event (e.g., wildfire, windstorm), on sites capable of succeeding towards a closed conifer canopy. Clearly, not all early-seral pre-forests in the PNW conform entirely to this condition and some attributes of this condition may well be provided by other forested and non-forested ecosystems. However, this *archetype* does exemplify the distinction between early-seral pre-forests and other similar ecosystems, and therefore should best reflect the evolved affinity plants and animals may have toward this forest succession state in the PNW. Based on this archetype we posit that the primary structural attributes of early-seral pre-forest in the PNW are: (1) abundant, co-dominant, short-statured broadleaf vegetation associated with a lack of conifer canopy closure, and (2) abundant biological legacies (residual structures from the pre-disturbance ecosystem; Franklin et al., 2000) dominated by a hyper-abundance of large snags and logs.

In the PNW, vegetation rapidly fills the growing space created by a canopy-opening disturbance. Until the new conifer canopy attains height and re-closes, the new stand can be co-dominated by a diversity of life forms including shrubs, hardwoods, conifers, herbs, and graminoids (Franklin et al., 2002). Virtually all studies of unmanaged succession following severe disturbances in the PNW report early dominance by woody shrubs or hardwoods, such as *Ceanothus* and *Alnus*, and a peak in abundance or diversity of graminoids and many herbs (e.g., Bailey and Poulton, 1968; Franklin and Dyrness, 1988; Halpern, 1988, 1989; Donato et al., 2009a,b). This co-dominance by a range of life forms effectively distinguishes early-seral pre-forest communities from the entire rest of the sere in most upland sites, which are heavily conifer-dominated from the competitive-exclusion through old-growth stages. This unique abundance can translate to system-level differences in foliage characteristics, flower and fruit abundance, trophic transfer (ecosystem energetics), and overall stature (see Campbell and Donato, *this issue*).

Biological legacies are the delimiting factor between the two basic kinds of succession, primary (no extant legacies) and secondary (some type of legacy, even if just soil elements). Snags and

down wood are perhaps the most conspicuous example, providing key structural elements in early-seral ecosystems (Franklin et al., 2002; Swanson et al., 2011). Because natural disturbances rarely consume much large-wood biomass (Campbell et al., 2007; Donato et al., 2013), the period following disturbance often represents a period of peak volumes for down wood and snags, often by several-fold (Harmon et al., 1986; Spies et al., 1988). Dead wood is a key habitat feature for several taxa including birds and bryophytes, and represents most of the organic matter present on the soil surface in burned sites. Efforts to make timber harvest emulate natural disturbance regimes generally include retention of snags and down woody debris (Franklin et al., 1997; Franklin et al., 2007) in order to retain functionality associated with late-seral forest (Aubry et al., 2009); however this retention also serves to enhance species richness during the post-harvest early-seral period (Rosenwald and Lohmus, 2008), although responses may vary among taxonomic groups (Sullivan et al., 2008). Surviving individuals (including scattered large trees) can be another important structural feature of naturally generated early-seral pre-forests. However, the functionality of these survivors is dependent on the context of disturbance severity and actually can serve as an element of continuity with, rather than distinction from, older (i.e., pre-disturbance) forest stages. Large wood can function in a similar sense, since it is also present in old forests, but most studies of dead wood succession in the PNW show a clear several-fold spike in large wood abundance in post-disturbance stands that help distinguish them from older stages (e.g., Spies et al., 1988).

In the following sections, we explore associations of various flora and fauna with early post-disturbance settings, focusing particularly on species affinity toward broadleaf vegetation and legacy wood abundance. Some accounts involve associations with broadleaf vegetation and legacy wood as provided by other forest condition classes including recently-harvested forests, partially-disturbed forests, and ecotones between forest and non-forest ecosystems. Doing so allows us to expand our information base from the paucity of studies conducted on archetypical early-seral pre-forest in the region and speaks directly to the structures that may attract and provide for early-seral associates.

3. Flora

Many herbs, grasses, bryophytes, shrubs, and tree species achieve their greatest absolute or relative abundance during the early-seral pre-forest stage of succession in the PNW (Franklin and Dyrness, 1988). A common dynamic following canopy-opening disturbances is a gradual, decades-long conifer establishment period (Franklin and Hemstrom, 1981; Stewart, 1986; Tappeiner et al., 1997; Poage and Tappeiner, 2002; Shatford et al., 2007; Poage et al., 2009; Tepley et al., 2013), which allows non-coniferous vegetation to dominate or co-dominate during the ~10–50 years prior to full canopy closure. Early-seral pre-forest vegetation varies with vegetation zones, as reviewed by Franklin and Dyrness (1988). *Rubus*, *Ceanothus*, *Gaultheria*, and *Rhododendron* are frequent in disturbed sites at low elevations in the west Cascades, while *Vaccinium*, *Spirea*, *Epilobium*, and the monocot *Xerophyllum tenax* are common at higher elevations. In the interior Northwest, *Physocarpus malvaceus*, *Ceanothus sanguineus*, and grasses are frequent early-seral associates.

Following one of the most famed disturbances in the region's history, the 100,000-hectare 1933 Tillamook Burn in the Oregon Coast Range, several distinct seral communities were identified nearly 3 decades after the fire. These communities varied by topographic setting and were often dominated by hardwoods including *Alnus rubra* (red alder), *Acer macrophyllum* (bigleaf maple), and *Acer circinatum* (vine maple); with various levels of the shrubs

Vaccinium parvifolium (red huckleberry), *Rubus parviflorus* (thimbleberry), and *Gaultheria shallon* (salal); the ferns *Polystichum munitum* (swordfern) and *Pteridium aquilinum* (bracken fern); and the herbs *Lotus crassifolius* (big deervetch) and *Trientalis latifolia* (western starflower) (Bailey and Poulton, 1968). Similarly, following fires in the northern Rocky Mountains of Idaho and Montana, post-fire early-seral pre-forest communities are typically dominated by shrubs in the genera *Alnus*, *Ceanothus*, *Holodiscus*, *Rubus*, *Salix*, and *Vaccinium* (Mueggler, 1965). Across several fires in the northern Rockies, Stickney (1990a,b) describes a 5- to 10-year period of herb/graminoid dominance, especially by *Epilobium angustifolium* (fireweed), *Lupinus argenteus* (silvery lupine), and *Calamagrostis rubescens* (pinegrass), followed by a multi-decade period of dominance by *Ceanothus velutinus* (snowbrush) and developing conifer saplings. Certain *Vaccinium* species, such as *V. membranaceum*, attain by far their greatest abundance and fruit productivity in open and/or disturbed sites (Anzinger, 2002; Martin, 1980).

Many studies of early vegetation succession in the PNW have been conducted following clearcut logging or a combined sequence of logging and burning, which, depending on subsequent vegetation management, can also exhibit a prolonged period of non-conifer dominance. On clearcut sites in the western Oregon Cascades, a peak in vegetation cover occurred at age 10–20 years of shrub genera such as *Rhododendron*, *Vaccinium*, *Rubus*, and *Ceanothus*, along with the important browse herb *Epilobium angustifolium* (Schoonmaker and McKee, 1988). Logged and burned sites in the Oregon Cascades were reported to undergo a similar trajectory, with *Epilobium angustifolium*, *E. paniculatum* (tall willowherb), *Rubus ursinus* (trailing blackberry), *Linnaea borealis* (twinflower), *Acer circinatum*, *Ceanothus velutinus* and *Senecio sylvaticus* (wood groundsel) increasing in the first 5 years after disturbance (Dyrness, 1973). A brief pulse of ruderal herbs followed by colonization and prolonged abundance of *Ceanothus*, *Rubus*, *Salix* (willow), *Epilobium angustifolium*, and others was observed following logging in the western Cascades of Oregon (Halpern, 1988, 1989). Across a 73-year chronosequence after logging and burning, the highest plant diversity occurred at 5 years of age in Douglas-fir forests of the western Washington Cascades (Long, 1977).

Bryophytes achieve higher diversity with a greater diversity of substrates (Rambo, 2001), such as exposed mineral soil, hardwood tree bases, and well-decayed coarse woody debris. Many of these substrates are present in early succession, and some bryophytes are very competitive colonizers of post-disturbance environments. For example, the moss *Funaria hygrometrica* is a region-wide post-fire colonizer, and often occurs with the thallose liverwort *Marchantia polymorpha* (Hoffman, 1966). McCune and Antos (1982), studying seral development of epiphyte communities on forest sites in northwestern Montana, associated species of *Bryoria*, *Cetraria*, and *Hypogymnia* with young stands of moderately open canopies, noting the role of high amounts of light and high moisture variability as being important factors in early succession for epiphytes. Most mosses, however, tend to increase in percent cover and biomass with increasing stand age, becoming especially important later in succession (McCune and Antos, 1982; Rambo and Muir, 1998).

The length of the early-seral pre-forest stage, and the vegetation that dominates therein, can vary widely depending on subsequent disturbances or tree regeneration patterns. Although slow tree establishment has been suggested as the norm in the PNW, rapid natural tree regeneration has also been reported, following wildfire events ranging from the western Washington Cascades (Winter et al., 2002) to Vancouver Island (Crown and Brett, 1975) to the Olympic Mountains (Huff, 1995). Following a severe autumn wildfire in the western Oregon Cascades, aerial seed banks on fire-killed Douglas-fir resulted in rapid and dense tree regeneration

(Larson and Franklin, 2005); this dense establishment continued for the first 14 years post-fire (Brown et al., 2013). These rapidly regenerating sites may support less abundant broadleaf and herbaceous components, and for a shorter time period. Conversely, “reburns” early in succession may lead to extended tree establishment periods (Bailey and Poulton, 1968; Franklin and Hemstrom, 1981). Significantly higher variability in tree establishment dates have occurred following reburn events, for example in the Siououx watershed of the central Washington Cascades (Gray and Franklin, 1997). A reburn in the Siskiyou Mountains of southwest Oregon reset tree regeneration timing but otherwise led to similar densities than after a single burn; however, woody shrubs were initially less dominant after a reburn and herbaceous cover was greater (Donato et al., 2009a,b).

A key aspect of the above studies is that, although most experienced no significant post-disturbance management, the disturbances themselves ranged from wildfires to clearcutting or some combination of logging and prescribed fire. The degree to which early-seral plant communities differ between sites originating from natural versus anthropogenic disturbances has scarcely been explored. The findings of at least one study suggest similarity in some vegetation components between natural and human-caused disturbances (Kayes et al., 2010); however, specific comparisons between these communities are few. Of particular relevance is whether post-disturbance vegetation management – especially dense planting of conifers and spraying of broadleaf vegetation – leads to markedly different early-seral pre-forest communities in terms of key species abundances, frequencies, duration of dominance, and especially ecosystem function. Many early-seral broadleaf species are trophically important forage or fruiting shrubs (Campbell and Donato, this issue), provide critical habitat (Hagar, 2007; Betts et al., 2010), or are important for nutrient cycling (e.g., nitrogen fixation by *Ceanothus*) and other values (e.g., nectar provision to pollinators by *E. angustifolium*). These questions of early-seral composition and related function constitute an important direction for future research.

Although there are several plant species common to the above studies, the question remains: Are there actual plant indicators specific to naturally regenerating early-seral pre-forests? For the most part, the species reported in these studies can also be found in mature and older forests (Halpern and Spies, 1995). The majority of findings suggest an ‘initial floristics’ model (Egler, 1954), in which most or all species are present throughout succession, but change in relative abundance at different stages (e.g., Halpern, 1989). Nevertheless, some studies suggest unique compositional attributes of early-seral pre-forest sites. For example, in mid-montane conifer forests in the northern Rockies, a number of vascular plant species occur primarily in early-seral pre-forest communities, including some species of *Vaccinium*, *Spirea* (steplebush), *Amelanchier* (serviceberry), *Fragaria* (wild strawberry), *Xerophyllum* (beargrass), and *Anaphalis* (pearly everlasting) (Habeck, 1968). The literature generally notes a decline in frequency and cover of these plants as conifer crowns expand and close. At least one species, *Senecio sylvaticus* (wood groundsel), is strongly associated with the first few years following disturbance such as fire, and rapidly declines thereafter (Halpern et al., 1997). One of the few studies in the PNW to apply indicator species analysis to quantitatively distinguish plants in pre-forest versus closed-canopy communities was conducted in the Siskiyou Mountains (Donato et al., 2009b). Strong indicators of sites experiencing one or two severe wildfires included the herbs *Pteridium aquilinum*, *Trientalis latifolia*, and *Vancouveria hexandra* (inside-out flower), shrubs in the genera *Rubus* and *Symphoricarpos*, as well as graminoid species (Donato et al., 2009b) – i.e., several of the components reported as important in the studies mentioned above. Rambo and Muir (1998) also identified several bryophytes associated with young hardwoods and

dead wood (e.g., *Neckera*, *Orthotrichum*, *Porella*, and *Radula* species). Nevertheless, the relative paucity of multi-dimensional or quantitative indicator analyses that distinguish early-seral pre-forests from closed-canopy community suggests an important direction for future research in PNW forests.

4. Fauna

Robust populations (and occasionally, highest abundances) of many species are found primarily in open or recently disturbed forest areas. Early-seral faunal associations will vary by plant association or community, as well as across elevational gradients and from coastal to interior regions. Most natural disturbances generate abundant snags and down woody debris, while prolonged periods of high light availability stimulate maximal foliage, flower, or fruit production for many plant species. Both of these processes result in positive responses from members of the vertebrate (Litvaitis, 1993; Bunnell, 1995; Kie et al., 2003) and invertebrate (Hammond and Miller, 1998; Bouget and Duelli, 2004; Hagar, 2007) components of the fauna. Birds are among the most studied vertebrates in post-disturbance ecosystems, and many are characteristic of early-seral pre-forest and/or broadleaf-dominated conditions (Meslow, 1978; Hagar, 2007). In the northern Rockies, fifteen bird species were found to occur primarily in recently burned areas, with one species, the black-backed woodpecker (*Picoides arcticus*), relatively restricted to post-fire early-seral environments due its abundance of newly generated snags (Hutto, 1995). Meslow (1978) examines seral patterns of 84 species of songbirds in western Oregon, and notes that a high proportion of the studied species use early-seral pre-forest stages (divided into a grass-forb stage and a shrub-sapling stage), and nearly half nest in these stages, including some that primarily nest in that stage, such as several sparrows and warblers, mountain quail (*Oreortyx pictus*), and the calliope hummingbird (*Stellula calliope*). Woodpeckers, especially, often have a limited period of high abundance during the first few years following severe wildfire, as they forage for insects on fire-killed or scorched trees (Covert-Bratland et al., 2006). Even in an industrial forest landscape in southwest Washington, characterized by relatively structurally simple and short-lived early-seral conditions, eight of 78 bird species were associated with early-seral conditions that declined as harvested stands matured: white-crowned sparrow (*Zonotrichia leucophrys*), song sparrow (*Melospiza melodia*), rufous-sided towhee (*Pipilo erythrophthalmus*), willow flycatcher (*Empidonax traillii*), black-headed grosbeak (*Pheucticus melanocephalus*), orange-crowned warbler (*Vermivora celata*), yellow-rumped warbler (*Dendroica coronata*), and American kestrel (*Falco sparverius*) (Bosakowski, 1997). Morrison and Meslow (1983) identify 22 nesting bird species and 21 foraging bird species, including raptors and mountain quail, in clearcuts in the Oregon Coast Range. In the interior Northwest, some avian guilds responded well to fire (e.g., cavity nesters, aerial insectivores, ground feeders), while some did not (e.g., bark gleaners) (Saab et al., 2003). In the Siskiyou Mountains, bird abundance was associated with broadleaf shrub height (Fontaine, 2007), and bird diversity was highest 17–18 years after severe fire, being higher than in mature forest (Fontaine et al., 2009). In southwest Washington, stands that had experienced disturbance, consisted of a mixture of small-diameter oak and pine, and had large live tree legacies had the highest number of bird species, especially neotropical migrants (Manuwal, 2003). A recent landmark study identified key thresholds of early-seral broadleaf cover, below which certain songbird species will decline (Betts et al., 2010), emphasizing the role of disturbance in creating a trophically productive early-seral broadleaf component. A number of these (e.g., rufous hummingbird (*Selasphorus rufus*), orange-crowned warbler, and purple finch (*Carpodacus purpureus*)) are already in decline regionally, as shown by breeding bird surveys

across their range. [Betts et al. \(2010\)](#) provide strong evidence associating their decline with reductions in early-seral broadleaf-dominated areas. Clearcuts and dispersed retention units, as silviculturally created variants of early-seral conditions, can benefit some native bird species, including the olive-sided flycatcher (*Contopus cooperi*), willow flycatcher (*Empidonax traillii*), and white-crowned sparrow ([Chambers et al., 1999](#)).

A number of mammals in forest landscapes display a preference for early-seral pre-forest conditions. Many ungulates, including blacktailed deer (*Odocoileus hemionus columbianus*) and North American elk (*Cervus elaphus*), preferentially use early-seral pre-forest areas with high availability of browse plants ([Nyberg and Janz, 1990](#); [Geist, 1998](#); [Toweill et al., 2002](#)). Blacktailed deer populations can increase to very high levels following large fire events in western Washington and Oregon, as shown following the Tillamook fires in the Oregon Coast Range, where deer densities had increased from 0.4 deer km⁻² to nearly 12 deer km⁻² in places ([Einarsen, 1946](#)). When feeding, elk tend to select for open, brushy habitats in forested landscapes of the northern Rocky Mountains ([Unsworth et al., 1998](#); [Irwin and Peek, 1983](#)) and the Oregon Coast Range ([Witmer and deCalesta, 1983](#)). These studies concurred that brushy clearcuts can contribute towards elk forage in these landscapes. Bighorn sheep throughout their North American range select for disturbed areas such as recent burns and clearcuts ([Risenhoover and Bailey, 1985](#); [Valdez and Krausman, 1999](#)). Moose (at least in the northern Rockies) do not share this affinity for early-seral pre-forest areas, instead using late-seral forest ([Pierce and Peek, 1984](#)).

As for carnivorous mammals, bears (*Ursus*) are an example of a wide-ranging generalist that frequently uses early-seral pre-forest communities for foraging ([Mace et al., 1996](#)). Berry-producing shrubs and other food sources achieve their highest yields in early-seral pre-forest communities, often 20–50 years post-disturbance ([Hamer, 1996](#)), and bears select for such areas ([Wielgus and Vernier, 2003](#)). Grizzly bears were found to prefer slowly recovering, naturally structured early-seral pre-forest habitats in preference to clearcuts ([Zager et al., 1983](#)). Buffaloberry (*Shepherdia canadensis*), an important source of soft mast for bears, produced greatest yields in post-fire environments with low tree cover, and areas where tree development was retarded by environmental factors experienced prolonged fruit production ([Hamer, 1996](#)). Although wolves and mountain lions do not directly require vegetative elements associated with early succession, these and other predators will indirectly benefit from the presence of productive early-seral patches of forage for their prey ([Wittmer et al., 2007](#); [Swanson et al., 2011](#)). An ongoing analysis (R.B. Wielgus and B.T. Maletzke, pers. comm., unpublished data) of lynx (*Lynx lynx*) in north-central Washington has revealed seasonal importance of young forest for lynx and their prey, the American snowshoe hare (*Lepus americanus*). Snowshoe hares were reported to prefer high cover by shrubs and conifers at the end of the early-seral pre-forest period, but the value of the early-seral patches is dependent on the surrounding landscape context ([Thornton et al., 2012](#)). Lynx reportedly use early-seral pre-forest patches that regenerate at a high conifer density ([Bull et al., 2001](#)), demonstrating that not all species with ties to early succession are benefitted by a prolonged pre-crown closure stage.

Small mammals show distinct seral assemblages following many kinds of disturbance. Following clearcutting and broadcast burning in Oregon's Cascade Range, late seral species such as northern flying squirrels (*Glaucomys sabrinus*) disappeared, while generalist and early-seral mammals such as the California ground squirrel (*Spermophilus beecheyi*), deer mouse (*Peromyscus maniculatus*), Townsend's chipmunk (*Eutamias townsendii*) increased ([Gashwiler, 1970](#)). Flying squirrels (*Glaucomys sabrinus*), a prey species of the northern spotted owl, tend to avoid open or

early-seral areas ([Ritchie et al., 2009](#)). On clearcut sites in northern Idaho, [Scrivner and Smith \(1984\)](#) found variable responses to clearcutting, with red-tailed chipmunks (*Eutamias ruficaudus*) and deer mice (*Peromyscus maniculatus*) experiencing some increases in pre-crown closure stands. The western jumping mouse (*Zapus princeps*) was reported to benefit from "alder-willow thickets", which are often elements of natural early-seral pre-forest communities. No significant difference in chipmunk abundance was found between young and mature stands west of the Cascade crest ([Hayes et al., 1995](#)); the highest abundances were in either old stands or young stands with abundant salal (*Gaultheria shallon*), underlining the importance of shrub communities. [Cole et al. \(1998\)](#) found that creeping voles (*Microtus oregoni*) and vagrant shrews (*Sorex vagrans*) capture rates increased within 2 years of clearcut logging, while other species declined or experienced no change. Lower bat activity has been found in young forests, but the 0–75 year age range used to define young forests means that closed-canopy, stem-exclusion stands were the probable subjects, not necessarily those representative of a diversely structured early-seral pre-forest condition ([Thomas, 1988](#)). Evidence from other regions ([Loeb and O'Keefe, 2011](#)) suggests that open areas may play an important role in bat foraging ecology in the PNW.

Reptiles and amphibians often display responses to seral development ([Bury and Corn, 1988](#)). In one study, young stands (age 5–10) in western Oregon forests yielded the only observations of garter snakes (*Thamnophis* spp.) and a disproportionate abundance of the northern alligator lizard (*Elgaria coerulea principis*) ([Gomez and Anthony, 1996](#)). Most of the amphibians in their study increased with increasing stand developmental stage, but two species (rough-skinned newt, *Taricha granulosa*, and western red-backed salamander, *Plethodon vehiculum*) were associated with deciduous stands, a stand type often associated with early succession. Amphibians display variable responses to disturbance ([Pilliod et al., 2003](#)), but in general do not benefit from the open conditions associated with early-successional stages. Such conditions may constitute a sink habitat for some amphibians ([Welsh et al., 2008](#)) due to loss of microclimatic protection and other factors. In northern California, clearcutting was observed to eliminate or greatly reduce amphibians from forest stands ([Welsh et al., 2008](#)). In coastal British Columbia, [Dupuis et al. \(1995\)](#) found a six-fold reduction in western red-backed salamanders in young stands (clearcut, age 5–6 or 17–18) compared to old-growth stands (age 380–500+). [Cole et al. \(1997\)](#) documented decreases in three of six amphibian species in a study of the effects of clearcutting in the Oregon Coast range. They did note an association of amphibians with red alder, a short-lived broadleaf tree highly associated with disturbance and the early-seral period. Some amphibians, such as the western toad (*Bufo boreas*), can increase following disturbance such as wildfire ([Guscio et al., 2008](#)) or volcanic eruption ([Crisafulli et al., 2005](#)).

While fish are not tightly dependent on early-seral pre-forest conditions, their abundance and biomass may increase following large disturbance events ([Howell, 2006](#)). This is likely due to enhanced primary productivity in streams, benefitting aquatic organisms in higher trophic levels. A review by [Gresswell \(1999\)](#) revealed that responses by fish populations were dependent on fire severity, whether debris torrents occurred following fire, and other factors, but noted that in many cases, post-fire fish biomass exceeded levels in unburned forests.

Insects contribute tremendously to species diversity in ecosystems worldwide ([Wilson, 1988](#)). In the PNW, a number of insects are associated with early-seral pre-forest areas. A significant number of uncommon to rare moth species have been associated with host plants such as *Vaccinium*, *Alnus*, and *Aquilegia* (columbine) ([Miller et al., 2003](#)), all of which often increase early in succession. [Miller et al. \(2003\)](#) suggest that early-seral areas play a role in

maintaining these species. Miller and Hammond (2007) review butterfly and moth species of conservation concern in the forests of the PNW, concluding that early-seral pre-forest patches make a crucial contribution to maintenance of these organisms in the regional landscape. Some taxa may require, or greatly benefit from, the co-occurrence of certain structural and compositional attributes of early-seral preforest. Some of the most important insect pollinators of beargrass (*Xerophyllum tenax*), such as *Cosmosalia chrysocoma* (Coleoptera: Chrysomelidae) and certain hover flies (Diptera: Syrphidae), use dead wood as a larval habitat feature (Hummel et al., 2012). The increase in beargrass abundance and flowering (Shebitz et al., 2008), combined with the abundance of woody debris in structurally complex early succession (Harmon et al., 1986), would presumably benefit these pollinators, with corresponding benefits to the beargrass population.

Overall, across several taxa there appear to be more established strong associates, or indicators, of structurally complex early-seral pre-forest conditions for wildlife than for plants. A key uncertainty for wildlife habitat relations is the degree to which early-seral preforests provide unique versus similar habitat function to other open habitat types such as meadows and balds in otherwise forested landscapes. Besides the primary difference that meadows and balds typically lack tree-derived structures (e.g., legacies), there are often floristic differences driven by site characteristics such as soil moisture and site climate (Franklin and Dyrness, 1988; Miller and Halpern, 1998). However, for some taxa, there may be an overlap in function due to the dominance of non-tree vegetation (e.g., abundance of flowering plants) in both types of open habitat.

5. Species of specific conservation concern

In this section we turn to vertebrate and invertebrate wildlife species of special conservation concern, to elucidate which of these especially management-relevant species are in some way dependent upon, or facultatively use, early-seral pre-forest. We examined the state-level species of concern or monitoring lists for Washington (<http://wdfw.wa.gov/conservation/endangered/status/SM/>), Oregon (http://www.dfw.state.or.us/wildlife/diversity/species/threatened_endangered_species.asp), and California (http://www.dfg.ca.gov/wildlife/nongame/t_e_spp/). A literature search was conducted during calendar year 2013 using Web of

Science (Thomson Reuters, New York, NY; accessed via Washington State University's portal) and Google Scholar (Google Inc., Mountain View, CA) to determine which species occurred in or adjacent to forested areas, and defined these as "selectors" (thus excluding species occurring in marine, desert, or other habitat types where forest succession is not a factor in habitat dependencies). We then searched the relevant literature including peer-reviewed, literature, Forest Service-BLM Species Fact Sheets, Forest Service General Technical Reports, and taxon-specific resources such as the webpage of the Xerces Society for Invertebrate Conservation (www.xerces.org), as well as references cited in already obtained literature for descriptions of habitat preference or occurrence. Keywords used to link biological associates to early-seral communities include "early-seral", "post-fire", "avalanche tracks", "windstorm", "clearcut", and "young stands/young forest". Obligatory dependence on early-seral communities was classified in terms of individual species directly mentioned in the literature to rely on such habitat to fulfill a critical life history requirement such as nesting, roosting, grazing or predation, or those that were indicated as strongly associated with some process, structure, or floristic element that is strongly tied to early-seral pre-forest environments (e.g., larval host requires early-seral conditions). Overall, we were conservative in our classification of early-seral obligates and even partial/facultative users; simple recorded occurrence of a species in a habitat type did not necessarily qualify it as an obligate species or a facultative/partial user of that type.

Eight-hundred sixty-five occurrences of species within the three states were assessed (species could occur more than once in this list, if listed in separate states). They were divided among seventeen habitat types: alpine and subalpine ($n = 6$), cave ($n = 6$), desert ($n = 7$), edaphic open areas ($n = 3$), disturbed forest ($n = 22$), forest ($n = 75$), mature forest ($n = 36$), forested wetlands or riparian areas ($n = 18$), freshwater ($n = 219$), grass/shrublands ($n = 71$), littoral ($n = 6$), marine ($n = 102$), mosaic ($n = 163$), perennially open habitats ($n = 69$), savanna ($n = 10$), waterfall ($n = 2$), and wetlands ($n = 50$). Marine and most freshwater species were excluded from further analysis. Four hundred and thirty-six species were considered selectors for forest habitat, but 35 were excluded from further analysis due to insufficient data on habitat requirements.

Only two of the state-listed freshwater species had positive associations (partial use) of early-seral environments (bull trout, *Salvelinus confluentis*, and Pacific pond turtle, *Actinemys*

Table 1
Numbers, proportions (in parentheses), and associations of state-listed species relative to early-seral habitat on forested sites in the three states (three species had insufficient data to make a determination). Note that row proportions will not add to one, since mature forest obligates will fall under the 'No use of ESFE' category.

	No use of ESFE	Partial/fac. use	ESFE Obligate	Mature Forest Obl.
N. California	9 (0.26)	25 (0.71)	1 (0.03)	4 (0.11)
Oregon	81 (0.43)	96 (0.51)	12 (0.06)	16 (0.08)
Washington	76 (0.39)	106 (0.55)	12 (0.06)	16 (0.08)

Table 2
Numbers, proportions (in parentheses), and associations of state-listed taxonomic groups relative to early-seral habitat on forested sites in the three states (three species had insufficient data to make a determination). Note that row proportions will not add to one, since mature forest obligates will fall under the 'No use of ESFE' category. One species may be listed in more than one state.

	No use	Partial/fac. use	ESFE Obligate	Mature Forest Obl.
Amphibian	21 (0.64)	12 (0.36)	0 (0.0)	3 (0.09)
Annelid	2 (1.00)	0 (0.00)	0 (0.00)	0 (0.00)
Bird	42 (0.39)	57 (0.52)	10 (0.09)	15 (0.14)
Butterfly or Moth	7 (0.09)	61 (0.80)	8 (0.11)	2 (0.03)
Fish	0 (0.00)	2 (1.00)	0 (0.00)	0 (0.00)
Mammal	16 (0.20)	63 (0.79)	1 (0.01)	6 (0.08)
Mollusk	26 (0.79)	7 (0.21)	0 (0.00)	6 (0.18)
Other Insect	46 (0.68)	19 (0.28)	3 (0.04)	4 (0.06)
Reptile	5 (0.36)	9 (0.64)	0 (0.00)	0 (0.00)

Table 3

State conservation-list species from Washington, Oregon, and California associated with mature and early-seral pre-forest conditions.

Species	Group	States listed	Habitat requirements	References
<i>Mature forest species</i>				
Rocky Mountain tailed frog (<i>Ascaphus montanus</i>)	Amphibian	WA	Coarse substrates, cold water in forested watersheds	Hawkins et al. (1988) and Welsh (1990)
Cascade torrent salamander (<i>Rhyacotriton cascadae</i>)	Amphibian	WA	Forested small streams	Steele et al. (2003)
Columbia torrent salamander (<i>Rhyacotriton kezeri</i>)	Amphibian	WA	Shaded watercourses	Grialou et al. (2000)
Northern goshawk (<i>Accipiter gentilis</i>)	Bird	WA, OR	Mature forest for nesting	Reynolds et al. (1982) and Graham et al. (1999)
Boreal owl (<i>Aegolius funereus</i>)	Bird	WA, OR	Mature forest	Hayward and Verner (1994)
Marbled murrelet (<i>Brachyramphus marmoratus</i>)	Bird	WA, OR, CA	Mature forest in proximity to coast	Grenier and Nelson (1995)
Pileated woodpecker (<i>Dryocopus pileatus</i>)	Bird	WA	Generally mature forest with large-diameter snags	Huff et al. (2005), Bull and Meslow (1977) and Bull and Holthausen (1993)
Flammulated owl (<i>Otus flammeolus</i>)	Bird	OR	Structurally complex forest with small mammal prey	Hayward and Verner (1994)
Great gray owl (<i>Strix nebulosa</i>)	Bird	WA, OR, CA	Structurally complex older forest for nesting and other activities (<i>note: uses ESPF or meadows for some foraging</i>)	Hayward and Verner (1994) and Bull and Henjum (1990)
Northern spotted owl (<i>Strix occidentalis caurina</i>)	Bird	WA, OR, CA	Structurally complex forest with small mammal prey	Meyer et al. (1998), Olson et al. (2004) and Glenn et al. (2004)
Johnson's hairstreak (<i>Mitoura johnsoni</i> , syn. <i>Callophrys johnsoni</i>)	Butterfly or Moth	WA, OR	Dwarf mistletoe in late-seral forest	Pyle (2002)
American marten (<i>Martes americana</i>)	Mammal	OR	Structurally complex forest with small mammal prey	Csuti et al. (1997) and Bull et al. (2005)
Fisher (<i>Martes pennanti</i>)	Mammal	WA, OR, CA	Structurally complex forest with small mammal prey	Fisher and Wilkinson (2005), Aubry and Lewis (2003), Aubry and Raley (2006) and Ruggiero et al. (1994)
Long-eared myotis (<i>Myotis evotis</i>)	Mammal	WA	Generally mature forest with large-diameter snags	Fisher and Wilkinson (2005) and Csuti et al. (1997)
Woodland caribou (<i>Rangifer tarandus</i>)	Mammal	WA	Large tracts of mature forest with abundant arboreal lichens	Rettie and Messier (2000), Wittmer et al. (2007) and Rominger et al. (1996)
Puget oregonian (<i>Cryptomastix devia</i>)	Mollusk	OR	Moist, shaded forest floors	Burke et al. (2000)
Malone jumping-slug (<i>Hemphillia malonei</i>)	Mollusk	OR	Moist, shaded forest floors	Burke et al. (2005)
Tillamook westernslug (<i>Hesperarion mariae</i>)	Mollusk	OR	Moist, shaded forest floors	Branson (1991)
Oregon megomphix (<i>Megomphix hemphilli</i>)	Mollusk	WA	Moist, shaded forest floors	Applegarth et al. (2000)
Crowned tightcoil (<i>Pristiloma pilsbryi</i>)	Mollusk	WA	Moist, shaded forest floors	Stone and Huff (2010)
Bluegray taildropper (<i>Prophysaon coeruleum</i>)	Mollusk	WA	Moist, shaded forest floors	Burke et al. (1999)
A caddisfly (<i>Lepania cascada</i>)	Other Insect	OR	Shaded watercourses	Anderson (1976) and Scheuering (2006)
A caddisfly (<i>Moselyana comosa</i>)	Other Insect	OR	Shaded watercourses	Huff and Vora (2010)
A caddisfly (<i>Namamyia plutonis</i>)	Other Insect	OR	Shaded watercourses	Scheuering (2006b)
Haddock's rhyacophilan caddisfly (<i>Rhyacophila haddocki</i>)	Other Insect	OR	Shaded watercourses	Wold (1974)
<i>Early-seral pre-forest species</i>				
Olive-sided flycatcher (<i>Contopus cooperi</i>)	Bird	OR	Abundant insect prey associated with broadleaf vegetation	Robertson and Hutto (2007)
Mountain quail (<i>Oreortyx pictus</i>)	Bird	OR	Abundant insect prey associated with broadleaf vegetation	Pope et al. (2004)
Black-backed woodpecker (<i>Picoides arcticus</i>)	Bird	WA, OR, CA	Insect prey and nesting in abundant snags	Hutto (1995), Koivula and Schmiegelow (2007), Hutto (2008) and Nappi and Drapeau (2009)
American three-toed woodpecker (<i>Picoides dorsalis</i>)	Bird	OR	Insect prey and nesting in abundant snags	Hutto (1995) and Koivula and Schmiegelow (2007)
Three-toed woodpecker (<i>Picoides tridactylus</i>)	Bird	WA	Insect prey and nesting in abundant snags	Hutto (1995) and Koivula and Schmiegelow (2007)
Western bluebird (<i>Sialia mexicana</i>)	Bird	WA, OR	Insect prey and nesting in abundant snags	Saab and Powell (2005) and Haggard and Gaines (2001)
Yellow-breasted chat (<i>Icteria virens</i>)	Bird	OR	Dense shrubs	Annand and Thompson (1997), Brawn et al. (2001) and Csuti et al. (1997)
Freija's fritillary (<i>Boloria freija freija</i>)	Butterfly or Moth	WA	Larval stage requires forb/herb/broadleaf vegetation	Pyle (2002) and James and Nunnallee (2011)

(continued on next page)

Table 3 (continued)

Species	Group	States listed	Habitat requirements	References
Pacuvius' duskywing (<i>Erynnis pacuvius lilius</i>)	Butterfly or Moth	WA	Larval stage requires forb/herb/broadleaf vegetation	Pyle (2002) and James and Nunnallee (2011)
Taylor's checkerspot (<i>Euphydryas editha taylori</i>)	Butterfly or Moth	WA	Larval stage requires forb/herb/broadleaf vegetation	Pyle (2002) and James and Nunnallee (2011)
Gillette's checkerspot (<i>Euphydryas gillettii</i>)	Butterfly or Moth	OR	Larval stage requires forb/herb/broadleaf vegetation	Pyle (2002) and James and Nunnallee (2011)
Western tiger swallowtail (<i>Papilio rutulus</i>)	Butterfly or Moth	WA	Larval stage requires forb/herb/broadleaf vegetation	Pyle (2002) and James and Nunnallee (2011)
Mardon skipper (<i>Polites mardon</i>)	Butterfly or Moth	WA	Larval stage requires forb/herb/broadleaf vegetation; meadows within forest matrix	Pyle (2002) and James and Nunnallee (2011)
Oregon silverspot butterfly (<i>Speyeria zerene hippolyta</i>)	Butterfly or Moth	WA	Larval stage requires fire-renewed coastal grassland on forest-potential sites	Pyle (2002), James and Nunnallee (2011) and Miller and Hammond (2007)
Sonora Skipper (<i>Polites sonora siris</i>)	Butterfly or Moth	OR	Forest openings with thistle (<i>Cirsium</i>), legumes, hawkbit (<i>Agoseris</i>).	Pyle (2002) and James and Nunnallee (2011)
Mazama (Western) pocket gopher (<i>Thomomys mazama</i>)	Mammal	WA	Early seral vegetation for food	Witmer et al. (1996), Verts and Carraway (2000) and Walker (1949)
A leaf-cutter bee (<i>Ashmeadiella sculleni</i>)	Other Insect	OR	Flowering individuals of <i>Penstemon</i> ; woody debris with beetle galleries	Shepherd (2005)
Siskiyou short-horned grasshopper (<i>Chloaltis aspasma</i>)	Other Insect	OR	Open grassy areas on disturbed forest sites	Rehn and Hebard (1919)
Douglas-fir plant bug (<i>Platylygus pseudotsugae</i>)	Other Insect	OR	Open regenerating Douglas-fir	Equihua-Martinez (1995)

marmorata). These were considered “selectors”, however, and therefore included in further analysis (see Table 1).

A large proportion of the species in all three states examined use early-successional stages to some degree (the ‘partial use’ classification). The proportion of species obligate (highly reliant on, or specialized to) early-seral pre-forest ecosystems did not differ strongly from the proportion reliant on mature forests in any of the three states examined (binomial test of proportions, California: $p = 0.08$, Oregon: $p = 0.16$, Washington: $p = 0.11$). Early-seral pre-forest and mature forest differed with respect to the type of taxonomic group that was favored (Table 2). Amphibians and mollusks, presumably due to their physiological requirements for moist and stable microclimates, were reliant on mature forest at a higher rate. Butterflies and moths, due to their general reliance on non-tree vegetation such as flowering shrubs and herbs (Pyle, 2002; Miller and Hammond, 2007; James and Nunnallee, 2011), showed the opposite trend of having more species reliant on early-seral pre-forest conditions. The species classified as obligate on early-seral pre-forest and mature forest are given in Table 3.

A number of species are very poorly described in the scientific literature, and we therefore were reluctant to make a determination of seral dependency. Some species (e.g., Columbia Gorge Caddisfly, *Neothremma andersonii*) are so tightly endemic to a given area, such as a single watershed, that their response to disturbance and seral development is indeterminate, or should not be inferred from the extant data. Other species are difficult to assess with respect to the very definition of early-seral communities. For example, should the Mazama ash and pumice fields that are part of the habitat of Leona's little blue butterfly (*Philotiella leona*) be considered a practically permanent geologic or edaphic substrate, or alternatively a very long-lasting form of early-seral forest habitat? (We here classify it as an edaphic habitat type, keeping short-term management relevance in mind). Some species are associated with conifers, but appear to prefer them in the early-seral setting (e.g., *Platylygus pseudotsugae*, Equihua-Martinez, 1995). Some conservation-dependent species require more than one compositional or structural attribute associated with early-seral pre-forest ecosystems. For example, *Ashmeadiella sculleni* (a leaf-cutter bee, Hymenoptera: Megachilidae) requires both *Penstemon* (Scrophulariaceae) flowers and snags or stumps with abundant beetle galleries

(Shepherd, 2005). Other occurrences of species in early-seral pre-forest communities represent marked deviations from their standard habitat requirements, and suggest that further research is warranted to clarify the possible role of early-seral habitat throughout the range of the species. For example, Beetle (1997) reported a number of land snails and a water snail (*Physa megalochlamys*) as positive respondents to the effects of the 1988 fires in aspen (*Populus tremuloides*) stands in the Yellowstone region. Yet other species, such as the white-headed woodpecker (*Picoides albolarvatus*), appear to require structures produced in late-seral stages (i.e., large diameter live conifers) but appear to experience greater reproductive rates in post-disturbance landscapes (Wightman et al., 2010). Finally, literature accounts for some of the species indicated that they used early-seral pre-forest in association with other types, at least in some portions of their range. This is the case for the northern spotted owl, which uses primarily late seral forest throughout its range, and is negatively impacted by wildfire (Clark et al., 2011). However, in the southern portion of its range, the spotted owl forages for dusky-footed woodrats (*Neotoma fuscipes*) in early-seral pre-forest adjacent to mature forest (Sakai and Noon, 1993; Folliard et al., 2000), or on prey emigrating from high-productivity early-seral pre-forest areas (Perry et al., 2011).

6. Conclusions and future research

Naturally occurring early-seral pre-forest communities appear to constitute a unique system on the seral spectrum for forested lands of the PNW. The structural attributes offered by this set of conditions provide habitat for a number of conservation-dependent species, as well as many species that are not rare, but are of substantial social and economic value (i.e., game animals such as deer, elk, and bear). Our research, while exploratory in nature, suggests that complex early-seral communities have importance on par with complex late-seral forests in providing habitat for conservation-listed species. Further research is needed on the habitat requirements of many species, however, to clarify the role of forest of different age, origin, and structural class. An additional challenge is that many studies that examine differences in biodiversity or species response across the seral report results from “young”,

“mature”, and “old/complex” forest, in which the “young” forest typically consists of closed-canopy conifer stands in the process of stem exclusion (e.g., Anthony et al., 1987; Bingham and Sawyer, 1991; Spies and Franklin, 1991; Bailey et al., 1998). Future research efforts on stands of differing age classes should very seriously consider the inclusion of pre-forest conditions as a treatment or observation group.

There appear to be more well-established “indicators” (strong associates) of early-seral pre-forest conditions for wildlife than for plant species, although there is evidence for seral dependencies for some plant species or assemblages. Key structural attributes of pre-forest span two axes of (1) vegetation co-dominance by a diversity of life forms and an abundance of broadleaf structure, and (2) biological legacies including exceptionally high quantities of large dead wood. Based on the structural attributes described here and elsewhere, traditional intensive forest management encouraging prompt reforestation and few legacies is unlikely to approximate the role of naturally generated early-seral conditions, although they may have value for specific taxa. Nevertheless, differences between managed/conifer-dominated and natural/broadleaf-dominated or mixed broadleaf/conifer early-seral forest ecosystems have not been thoroughly explored, either with respect to composition or related function. What proportion of the functions associated with early-seral pre-forest ecosystems is provided by the various types of early-seral communities, and their mixtures in the region, remains an extremely important direction for future research.

While not final due to the evolving state of knowledge on early-seral communities and the habitat dependencies of many wildlife species, the conclusions presented here suggest that early-seral conditions play an important role in maintaining a number of societally important values, including rare or conservation-dependent species. This analysis suggests that strategies to create or retain the elements of complex early-seral communities be implemented in forest management where the conservation of biological diversity (including rare or threatened species) is an objective.

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