Early Seral Forest in the Pacific Northwest: A Literature Review and Synthesis of Current Science

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Abstract

Early seral forest is attracting increasing attention from scientists and managers. This literature review, produced under contract to the United States Forest Service, addresses basic questions about this important seral stage in the forests of the Pacific Northwest (west and east of the Cascades Range). Generative processes, historic landscape abundance, ecological value, associated species (and their ecological adaptations and conservation status), landscape-scale considerations (including patch size), and issues relatied to forest management are central topics. In general, naturally structured early seral forest in the Pacific Northwest is important for many ecosystem services and species (including obligates and near-obligates), but has declined from historic landscape proportions.

Introduction

The topic of early seral forest is increasing in importance for forest managers, 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). Naturally structured and composed early seral forest communities, in many forest landscapes, maintain values that are not usually provided by other seral stages (Swanson et al. 2011). On lands belonging to the federal government, the question of creating or maintaining early seral forest communities via management or changes in management is of growing interest, especially where timber-dependent communities seek some form of timber harvest (Franklin and Johnson 2010). This literature review seeks to answer common questions land managers may have about early seral forest communities and their management in the forests of the Pacific Northwest.

Literature was located via Web of Science and Google Scholar, as well as by searching citation lists in pertinent papers. The geographic scope was held to the Pacific Northwest, here defined as the maritime temperate zone from northern California to southeast Alaska, and extending inland to western Montana. Literature pertaining to the southern Rocky Mountains of the USA, northern Alberta and northeastern British Columbia of Canada, and all of California save the northwestern coastal forests were generally excluded. Literature was generally drawn from this region, but references with general or overarching relevance may be taken from literature pertaining to other forest regions.

What natural processes result in early seral forest?

Fire, of high and mixed severity, is the dominant stand-replacing disturbance agent across the Pacific Northwest (Franklin and Hemstrom 1981, Agee 1993, Agee 1998), with some tree and shrub species contributing to the potential for future fire events as a means of persistence over time (Mutch 1970, Vogl 1973, Fonda et al. 1998). These disturbances create snags and down woody debris (Harmon et al. 1986), volatilize nutrients and biomass (Campbell et al. 2007), and open growing space for the establishment of new cohorts of shrubs, trees, and forbs (Oliver and Larson 1996). Fire has been a major disturbance process in the Pacific Northwest throughout the Quaternary epoch, even in relatively moist coastal systems (Long and Whitlock 2002, Gavin et al. 2003).

Wind is also a prominent disturbance factor in the forests of the Pacific Northwest (Franklin and Hemstrom 1981, Nowacki and Kramer 1998, Harcombe et al. 2004). Wind as a disturbance agent tends to superimpose a fine-scale mosaic pattern (Lertzman et al. 1996), frequently on a coarser mosaic created by large fire-created patches (Spies and Franklin 1989). Windthrow gaps of relatively small size may contribute to the persistence of mid-tolerant tree species such as Sitka spruce (Taylor 1990) as stands move into late succession. Large windstorms also occur, however, and may create a variant of early seral forests dominated by advanced regeneration of shade-tolerant trees and shrubs (Franklin et al. 2002). The relative importance of wind as a disturbance agent varies at both large and small spatial scales (Nowacki and Kramer 1998). Wimberly and Spies (2001), in their study area in coastal Oregon, found that wind disturbance is more frequent close to the coast, and on certain topographic positions with higher wind exposure. Forest management activities, especially the introduction of hard edges via clearcutting, can also influence wind as a disturbance agent, enhancing the size of wind-throw gaps and rate of formation (e.g., Sinton et al. 2000). Wind disturbance operates very differently from fire in that exposure of mineral soil or scarification is held to a minimum, and late-successional plants are released.

Volcanic eruption, while not historically viewed as a frequent disturbance, is a major disturbance agent in the Cascades Range of the Pacific Northwest. Yamaguchi (1983) cites two major eruptions at Mt. St. Helens in the central Washington Cascades that can be dated relatively precisely via dendrochronology: 1480 and 1800. This, along with the 1980 eruption, suggests a return interval that is not substantially longer than the fire return interval for the western hemlock and Pacific silver fir zones. The 1980 eruption of Mt. St. Helens may be one of the most pivotal events in the history of forest ecology, facilitating scientific understanding of the importance of biological legacies (Franklin et al. 2000) and encouraging scientists to acknowledge the ecological role of large, slowly recovering disturbed areas (Dale et al. 2005a). Studies of the effects of this eruption have included work on the patterns and processes associated with primary succession (e.g., del Moral et al. 1995), which is far less common than secondary succession in the Pacific Northwest. A volcanic eruption usually involves several different actual disturbance types, including pyroclastic flows, lahars/volcanic mudflows, and tephra deposition or ash fall (Crisafulli et al. 2005). The variable severity of each of these disturbances at variable distance from a volcano, and in different exposure settings, results in a diverse mosaic of post-disturbance conditions with variable survivorship or retention of living and dead organisms (del Moral et al. 2005). This sets the stage for a high diversity of developmental pathways in the resultant early seral landscape.

Snow avalanche, a gravity-driven translocation process, also creates early seral habitat. Franklin et al. (1988) describe avalanche disturbance as the second leading cause of stand replacement in the forests of Mount Rainier National Park, and this is likely to be a general finding in the snowy and steep domain of mid-high elevation forests of the Cascade Range. In a study from just outside the geographic scope of this review, Patten and Knight (1996) found that over 50% of their study area was affected by avalanche. Snow avalanche tends to produce a “late-succession” variant of early succession if infrequent, releasing snow-covered advanced regeneration of shade-tolerant trees, but may also maintain a disclimax condition dominated by disturbance obligates/associates such as *Alnus* and *Vaccinium* (Schaerer 1973, Butler 1979). While an important generator of early seral habitat at high elevation, snow avalanche may also constrain fire events by creating cross-slope fuel breaks (Dorner et al. 2002).

Insects and disease commonly kill trees in small-scale patches, but occasional large disturbances can be attributed to biotic agents of mortality. A key example is the mountain pine beetle outbreaks of the late 20th century and early 21st centuries in British Columbia and the Rocky Mountains of the USA (Aukema et al. 2006). Bark beetle (family Scolytidae) attack may follow fire events (Hood et al. 2007, Christiansen et al. 1987), contributing to the severity of disturbance, but insects may also increase the susceptibility of forest stands and landscapes to fire events

(McCullough et al. 1998). Astrup et al. (2008) report that, in the absence of subsequent disturbance, mountain pine beetle disturbances may lead to compositional shifts in forest structure, as substrate limitations favor previously-established true fir and spruce regeneration. Mountain pine beetle outbreaks can mimic fire in some of its overall structural effects, including the creation of large diameter snags and woody debris (Dordel et al. 2008).

An important operation of most types of natural disturbance is that biological legacies are created or retained in the disturbance phase, and these enrich the developing stand (Franklin et al. 2000, Franklin et al. 2002). Creation of woody debris (snags and down wood) and uproot structures such as pit-and-mound topography is an active effect of disturbance (Harmon et al. 1986, Maser et al. 1988), while retention of live trees, shrub/forb understories, and other elements of the biotic community results from uneven severities within a disturbance.

What percentage of the landscape has historically been in an early seral condition?

The percentage of the regional landscapes of the Pacific Northwest in early succession was a highly variable parameter, depending on location in the Pacific Northwest. Teensma et al. (1991; Figure 1) reconstructed the age-class distribution of forests in the 19th and 20th century for the Oregon coast range, noting that as much as 35% of the mapped landscape was in a "recently burned" condition in 1850. However, this proportion decreases by the end of the century as stands naturally restocked, only to increase again with such early 20th century events as the Tillamook Fire of 1933. Wimberly et al. 2000 employed parameters of the observed fire regime in forests of the Oregon coast range to model the proportion of landscape in late-successional and old growth status. They conclude that late seral forest fluctuated at provincial scales between 25 and 75% of the landscape, and never dropping below 5%. While the balance of the forest landscape might have been ambiguously divided between early seral and young stem-exclusion forests, it is reasonable to expect that much of the balance would have been in a true pre-crown closure condition. This assumption is based on the increasingly wide recognition that early seral conditions, as indicated by continued establishment of Douglas-fir, frequently took a century or more in historic landscapes (Poage et al. 2009). Takaoka and Swanson (2008) used historic and modern aerial photographs to assess change in the percentage of the greater Blue River region of the central Oregon Cascades represented by shrub fields and early seral conifer communities. They concluded that such early seral cover types decreased from about 5% of the landscape in the 1940's to about 2.5% of the contemporary landscape.

Return intervals for coastal and western Cascadian forests range from 150-600 years (Franklin and Hemstrom 1982, Franklin and Dyrness 1988, Morrison and Swanson 1990, Agee 1993). Time to crown closure (and therefore the cessation of the early seral phase) is highly variable in Northwestern forests (Franklin et al. 2002). Assuming a very conservative low-end estimate of 30 years to crown closure (see Tappeiner 1997 and Poage et al. 2009 for context on this assumption), this would suggest that at any one point in recent history, 5-20% of a given landscape would have been in an early seral condition. Note that this is an order-of-magnitude estimate that ignores topographic, edaphic, and climatic variability in real landscapes; Gavin et al. (2003) and many others point out that (especially in cooler, moister systems), fire is spatially constrained by variable fuel and moisture conditions as a result of aspect, topographic exposure, and other factors.

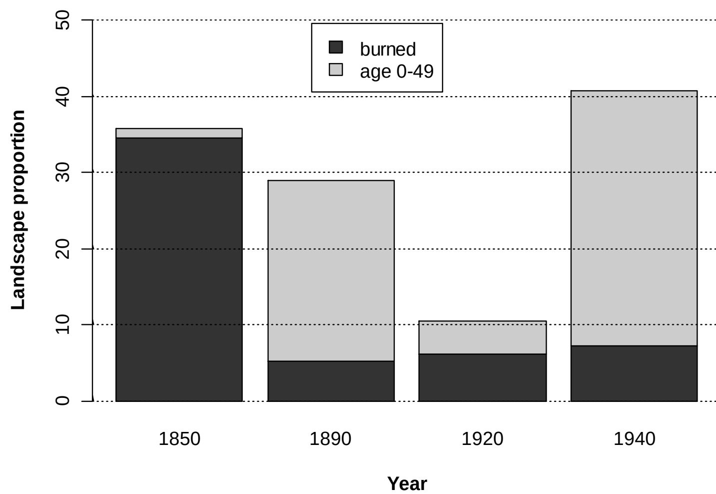

Figure 1. Historical landscape proportions of early seral types in the Oregon Coast Range. Note the high proportion of burned area in 1850; much of the age 0-49 in 1940 would have been from logging and thus likely less structurally rich and compositionally diverse than naturally occurring early seral habitat created earlier. *Drawn from data given by Teensma et al. (1991).*

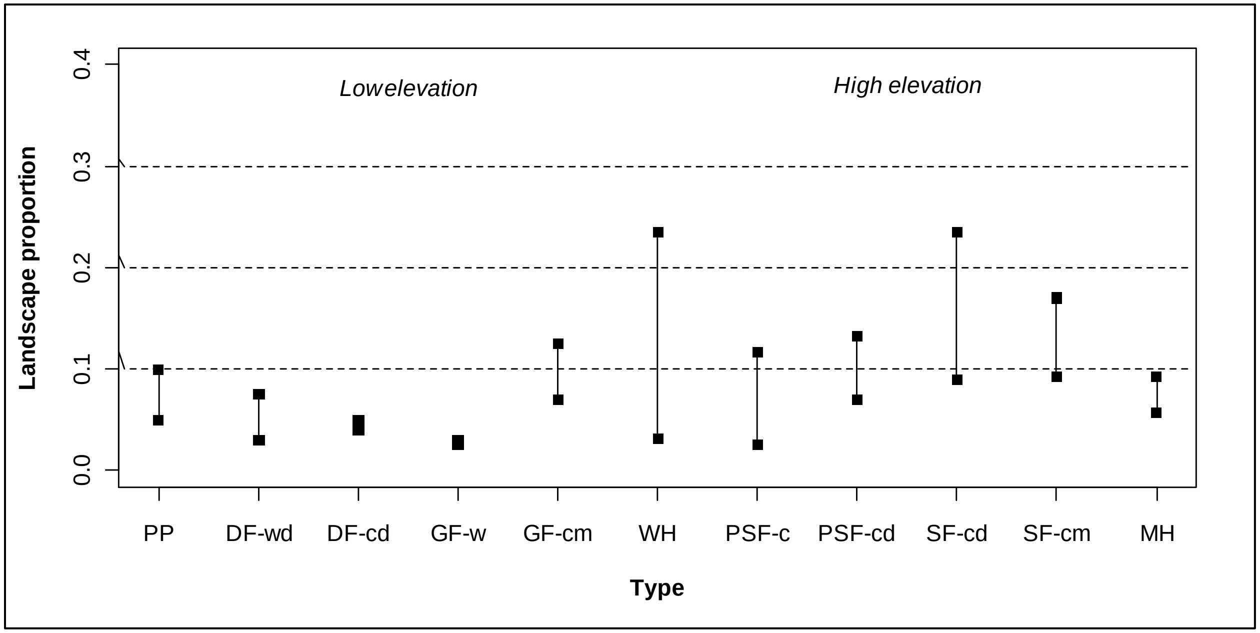

Figure 2. Historic range of variability in landscape proportion occupied by the shrub/sapling stage. PP=ponderosa pine; DF-wd= Douglas-fir, warm/dry; DF-cd=Douglas-fir, cold/dry; GF-w=grand fir, warm; GF-cm=grand fir, cool mesic; WH=western hemlock; PSF-c= Pacific silver fir, cool; PSF-cd=Pacific silver fir, cold/dry; SF-cd=subalpine fir, cold/dry; SF-cm= subalpine fir, cool/mesic; MH=mountain hemlock. *Drawn with data from Agee (2003)*.

Agee (2003) assessed the historic range of variability in landscape proportions of different seral classes across the main forest communities in the eastern Cascades. Shrub/seedling (generally early seral) communities ranged from 2-25% of many forest types (figure 2). Note that the warmer and/or drier systems at lower elevations typically had a much lower proportion in this stage, since low-severity fire, not high severity stand replacement fire, is the dominant disturbance type.

Some portions of the east Cascades domain that were historically influenced by low-severity fire have now, through the intertwined effects of fire suppression, cattle grazing, road construction, and their resulting impacts on forest demography and structure, come to be characterized by the potential for stand-replacing fire events (Hessburg and Agee 2003). In these situations, there is the potential for *more* large patches of early seral vegetation than under historical conditions, not less (Hessburg et al. 2005). However, the biota associated with these forests will likely benefit less from this outcome than from management designed to restore structures and patterns associated with the historic low- and mixed-severity fire regimes.

Marlon et al. (2012) report that less area has experienced fire during the 20th century than would be expected according statistical models of the climate-wildfire relationship, suggesting a deficit in mesic-site early seral forest communities as well as communities maintained by frequent fire (e.g., meadows, open ponderosa pine stands).

What are the characteristics of ecologically functional early seral forest?

The three primary attributes of ecosystems are composition, structure, and function. Functionality arises from the attributes of composition and structure, and thus will be addressed in parallel with those attributes in this section.

Compositional diversity of the vascular plant community (including forbs, shrubs, and trees) is a key attribute of early seral communities (Swanson et al. 2011). Many forbs, shrubs, and tree species achieve their greatest importance in naturally occurring areas of early succession in the Pacific Northwest (Franklin and Dyrness 1988). In the Tillamook Burn, Bailey and Poulton (1968) identified eight seral community types in different combinations of soil and topographic position, with *Gaultheria*, *Vaccinium*, *Rubus*, *Lotus*, *Pteridium*, *Elymus*, *Acer circinatum* and others in non-tree dominated types, and *Alnus rubra* and *Acer macrophyllum* in tree-dominated types. In northern Idaho, post-fire environments were rich in shrub species (many beneficial for ungulate browse), including members of *Alnus*, *Ceanothus*, *Holodiscus*, *Rubus*, *Salix*, *Vaccinium*, and many more (Mueggler 1965). Not all fires result in a long-lasting early seral stage. Following severe fall-season wildfire in the Oregon Cascades, Larson and Franklin (2005) describe regeneration by aerial seed banks by Douglas-fir, which may result in dense regeneration of Douglas-fir. A single fire event may tend to have denser, more immediate regeneration, while “reburn” events, or repeat fires that occur early in succession, may lead to extended tree establishment periods (Bailey and Poulton 1968, Gray and Franklin 1997). Gray and Franklin, in particular, found significantly higher variability in establishment dates following reburn events in the Siouxon watershed of the central Washington Cascades. Rapid and dense natural regeneration in coastal Northwestern systems appears to be relatively less common that more extended establishment periods (Stewart 1986, Tappeiner et al. 1997). Following volcanic eruption, forb and shrub diversity can increase to very high levels (Frenzen et al., *unpublished data*). This diversity of forbs, shrubs, and broadleaf trees highlights a major role of large disturbances in the conifer-dominated Pacific Northwest. Even following clearcutting, burning, and planting with a commercial conifer tree species such as Douglas-fir, there may be a period of enhanced shrub and forb cover. On clearcut sites in the western Oregon Cascades, Schoonmaker and McKee (1988) identified a peak in cover at stand age 10-20 of ecologically important shrubs such as *Rhododendron*, *Vaccinium*, *Rubus*, and *Ceanothus*, along with the important browse herb *Epilobium angustifolium*. Logged and burned sites in the Oregon Cascades underwent a similar trajectory, with *Epilobium angustifolium*, *E. paniculatum*, *Rubus ursinus*, *Linnea borealis*, *Acer circinatum*, *Ceanothus velutinus* and *Senecio sylvaticus* increasing in the first five years after disturbance (Dyrness 1973). Halpern (1989), also working in logged areas in the west Oregon Cascades, found a brief pulse of ruderal herbs is followed by colonization by, and fairly prolonged abundance of, *Ceanothus*, *Rubus*, *Salix*, *Epilobium angustifolium*, and others (Halpern 1989). Many of these are important for nutrient fixation or cycling (e.g., nitrogen fixation by Ceanothus), forage (*Ceanothus*, *Bromus*, *Salix*, *Rubus*), and other values (e.g., nectar provision to pollinators by *E. angustifolium*). Habeck (1968), examining seral trends in mid-montane conifer forests in the northern Rockies, reported that a number of vascular plant species occur primarily in pioneer and early seral stages, including *Vaccinium*, *Spirea*, *Amelanchier*, *Fragaria*, *Xerophyllum*, and *Anaphalis*. Many of these are trophically important fruiting shrubs. The literature generally notes a decline in frequency and cover of these plants as conifer crowns expand and close. Donato et al. (2009), working in early seral environments in southwest Oregon resulting from both single burn events and short-interval reburn events, describe communities with regenerating conifers (mostly *Pseudotsuga menziesii*, but with *Pinus attenuata* and *P. lambertiana* represented), hardwood trees and tall shrubs (including *Lithocarpus densiflorus*, *Arbutus menziesii*, *Ceanothus velutinus*, *Garrya*, and *Arctostaphylos*), low shrubs (including *Berberis*, *Rubus*, *Symphoricarpos*), and forbs (including *Achlys*, *Lotus*, *Pteridium*, *Vancouveria*). Many of the shrubs and forbs, especially, are important fruit and forage producers.

Provision of food resources via fruit and seed production is a very important role of early seral forest ecosystems. Huckleberries (genus *Vaccinium*) provide an excellent example, being culturally and ecologically important (Minore 1972, Minore and Dubrasich 1978). Anzinger (2002) discussed declines in cover and fruit production in big huckleberry (Vaccinium membranaceum) in the northern Oregon Cascades as a function of increasing overstory cover by conifers. Martin (1980) found that areas burned by wildfire 25-60 years previous, or clearcut harvested 8-15 years previous, had higher huckleberry production than older forest stands with higher canopy cover.

Biological legacies, living or dead residual structures from the pre-disturbance ecosystem (Franklin et al. 2000), are crucially important to early seral functionality. Their presence or absence is 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, occur and influence succession). Surviving organisms are highly influential, since their reproduction bypasses the often slow process of recolonization from outside the disturbed area. Keeton (2000) found significant spatial correlations between surviving shade-tolerant trees and shade-tolerant regeneration a century following landscape-scale wildfire in the south Washington Cascades. At Mt. St. Helens, very few plant or animal species were eliminated from the blast zone; organisms survived as perennating root systems, seeds, in underground refugia (e.g., animal burrows), under late-spring snowbanks, and in many other ways (Franklin 1990, Franklin et al. 2000, Crisafulli et al. 2005). Naturally, the age and structure of the pre-disturbance ecosystem will influence the types of legacy structures present in the post-disturbance early seral phase (Vierling et al. 2008).

Down woody debris and snags are key structural elements of highly functional early seral forest ecosystems (Swanson et al. 2011). The early seral phase following disturbance often represents a period of peak volumes for down wood and snags (Harmon et al. 1986); this is true for many other forest regions (e.g., Pedlar et al. 2002, Carmona et al. 2002). This may depend on the nature of the disturbance (e.g., reburns that consume woody debris; Spies et al. 1988). Efforts to model timber harvest on natural disturbance generally include retention of snags and down woody debris (Franklin et al. 1997, Franklin et al. 2007).

Nutrient fixation, transformation, and movement are often accelerated during early succession, as evinced by the classic study of clearcutting and nutrient export at Hubbard Brook (1968). McClain et al. (1998) discuss a number of important post-disturbance nutrient-related processes, such as nitrogen fixation by seral vegetation, nutrient export to aquatic ecosystems, and increases in foliage types (e.g., herbs) that enhance nutrient availability in terrestrial and adjacent aquatic systems.

Over longer time periods, spatially irregular development initiated early in succession, accompanied by a diversity of life-forms, may lead to structurally complex forests (Zenner 2005). Furthermore, the recently proposed 'precocity' pathway (Donato et al. 2011) states that diverse structure and spatial heterogeneity in early seral stands may actually accelerate the onset of structural and compositional attributes associated with late seral forests.

Habitat characteristics of early seral forest are also addressed by faunal group or by species in the following sections.

What species are tied specifically to that habitat type?

In this section, I will primarily address vertebrate species, since plant communities were addressed earlier. It is fitting to note that few species are absolutely obligate in early seral communities, but robust populations of many species are primarily found in early seral communities.

Certainly not all species prosper in ESFEs. For example, early seral forest may constitute a sink habitat for some amphibians (Welsh et al. 2008) due to loss of microclimatic protection and other factors, and flying squirrels (*Glaucomys sabrinus*), a prey species of the northern spotted owl, tends to avoid open or early seral areas (Ritchie et al. 2009). However, naturally structured ESFE with abundant biological legacies and a diverse early seral plant community can be rich in vertebrate species.

Bryophytes achieve higher diversity with a greater diversity of substrates (Rambo 2001), such as 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 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).

Many ungulates, including blacktailed deer (*Odocoileus hemionus columbianus*) and elk (*Cervus elaphus*), preferentially use early seral areas with high availability of browse plants (Nyberg and Janz 1990, Geist 1998, Toweill et al. 2002). Blacktailed deer populations can increase to quite high levels following large fire events in western Washington and Oregon, as shown following the Tillamook fires in western Oregon, where deer densities had increased from 1 deer mile^{-2} to more than 30 deer mile^{-2} in some 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 habitats, instead using late-seral forest (Pierce and Peek 1984).

Bears (Ursus) are wide-ranging generalists that frequently use early seral communities for foraging. Berry-producing shrubs and other food sources achieve their highest yields in early-seral communities, often 20-50 years post-disturbance (Hamer 1996), and bears select for such areas (Wielgus and Vernier 2003). Zager et al. (1983) found that grizzly bears preferred slowly recovering, naturally structured early seral habitats in preference to clearcuts. 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).

Many birds are characteristic of early seral habitats (Hagar et al. 1997). In the northern Rockies, Hutto (1995) found fifteen bird species occurring primarily in recently burned areas, with one species, the black-backed woodpecker (*Picoides arcticus*), relatively restricted to early seral post-fire environments. He also found that many species are relatively more abundant in post-fire environments, although they may not specifically select for them. Woodpeckers, especially, often have a limited period of high abundance during the first few years following severe wildfire (Covert-Bratland et al. 2006). Bosakowski (1996) examined breeding birds in relation to stand types and ages on an industrial forest landscape in southwest Washington. From a total of 78 species observed, he identified eight birds associated with early seral conditions that declined as harvested stands matured: white-crowned sparrow, song sparrow, rufus-sided towhee, willow flycatcher, black-headed grosbeak, orange-crowned warbler, yellow-rumped warbler, and American kestrel. Saab et al. (2003) reviewed bird response to fire in the interior Northwest, finding that some guilds responded well to fire (e.g., cavity nesters, aerial insectivores, ground feeders), while some did not (e.g., bark gleaners). In southwest Oregon, bird diversity appeared to be highest 17-18 years after severe fire, and was higher than in mature forest (Fontaine et al. 2009). Shrub and hardwood tree abundance, an important vegetation contributor to high bird diversity, may be enhanced by short-interval repeat burn events (Donato et al. 2009). Garry oak woodlands in southern Washington had a substantially greater richness of bird species than Douglas-fir dominated habitats in western Washington (Manuwal 2003). Stands that had experienced disturbance, consisted of a mixture of small-diameter oak and pine, and had large live tree legacies had the highest of bird species, especially neotropical migrants. Betts et al. (2010) performed a landmark study identifying thresholds of early seral broadleaf cover below which certain songbird species will decline. A number of these (e.g., rufous hummingbird, orange-crowned warbler, and purple finch) are already in decline, as shown by breeding bird surveys across their range. Betts et al. provide strong evidence associating their decline with reductions in early seral broadleaf habitats.

Although wolves and mountain lions do not directly require elements of succession, these and other predators will indirectly benefit from the presence of productive early seral patches of forage for their prey (Swanson et al. 2011). An ongoing analysis (R.B. Wielgus and B.T. Maletzke, *pers. comm.*) of lynx (*Lynx lynx*) in north-central Washington has revealed seasonal importance of early-seral forest for lynx and their prey, the American snowshoe hare (*Lepus americanus*). Bull et al. (2001) found that lynx use early-seral habitats that regenerate at a high conifer density, 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 Cascades 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). On clearcut sites in northern Idaho, Scrivner and Smith (1984) found variables 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 stages. Hayes et al. (1995) report no significant difference in chipmunk abundance between young stands and mature stands; they note that the highest abundances seen were in either old stands or young stands with abundant salal (*Gaultheria shallon*), underlining the importance of shrub communities.

Reptiles and amphibians often display seral tendencies. Gomez and Anthony (1996) studied reptiles and amphibians in five age classes of forest in western Oregon. They report that young stands (age 5-10) yielded the only observations of garter snakes (*Thamnophis* spp.) and a disproportionate abundance of the northern alligator lizard (*Elgaria coerulea principis*). 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 generally generated by early successional dynamics. 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. 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+). However, some amphibians, such as the western toad (Bufo boreas) do increase following disturbance such as wildfire (Guscio et al. 2008) or volcanic eruption (Crisafulli et al. 2005b).

While fish are not tightly dependent on early seral 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). In the Pacific Northwest, a number of insects are associated with early seral habitats. Miller et al. (2003) found a number of uncommon to rare moths to be associated with host plants such as *Vaccinium*, *Alnus*, and Aquilegium, all of which can increase in early succession. They suggest that early seral habitats play a role in maintaining these species. Miller and Hammond (2007) review butterfly and moth species of conservation concern in the forests of the Pacific Northwest, concluding that early seral habitats make a crucial contribution to maintenance of these organisms in the regional landscape.

Of those species, which are of conservation concern?

A search of the literature and lists of species of conservation concern at both state and federal levels reveal a large number of species that are either dependent on early seral habitat, use it for some aspect of their life history, or are able to utilize this habitat type opportunistically. Examples occur across almost all life forms and taxonomic groups, including trees, birds, mammals, herbs, and insects. Hagar (2007) identifies 78 species of vertebrate associated with non-coniferous vegetation; some of these are declining or otherwise of conservation concern or in a protected status.

Whitebark pine is threatened by the introduced white pine blister rust (Cronartium ribicola), extensive bark beetle outbreaks, and lack of suitable regeneration opportunity due to fire suppression (Keane et al. 1994, Campbell and Antos 2000). As noted earlier, this tree is favored by large disturbance events that confer a competitive advantage to organisms dispersed by animals. The western bluebird (Guinan et al. 2008) and the black-backed woodpecker (Hutto 1995) are bird species almost emblematic of early seral habitat, and are on several state-level conservation lists. Grizzly bears are of conservation concern, listed as "threatened" at the federal level in the United States. In the Pacific Northwest, both resident and anadromous species of fish (e.g., salmon, *Oncorhynchus*) figure prominently on lists of threatened, endangered, or monitored species; while few of these rely directly on early seral habitat, they may benefit from conservation planning that includes natural disturbance regimes (Reeves et al. 1995). A significant number of state-listed organisms associated with early seral habitats are lepidoptera (butterflies and moths), since their larval stages depend on herbs, shrubs, or broadleaf trees that occur primarily in early seral habitats, and adults may require floral nectar as a food source.

A number of species occupy fire-maintained disclimax forest types (e.g., Oregon oak savanna), and these have been negatively impacted by fire suppression and other factors. Examples include Fendler's blue butterfly (*Icaricia icarioides fenderi*) and golden paintbrush (*Castilleja laevisecta*). There are also many organisms that may be impacted negatively by forest encroachment onto formerly open habitat (e.g., loggerhead shrike, *Lanius ludovicianus,* or the grasshopper sparrow, *Ammodramus savannarum*), but are not addressed in this document, since they do not regularly use early seral forest habitat per se.

What are the ecological adaptations of species associated with early seral forest?

Early seral plants frequently have indeterminate growth patterns that provide them with responsiveness to environmental stochasticity in the highly variable early seral environment, whereas late-successional species frequently have determinate growth patterns and relatively invariant leaf characteristics (Koike 1990). The harsh and variable light and temperature conditions encountered in early seral habitats confer an advantage on species with protective structures or biochemical constitution. Prairie lupine (*Lupinus lepidus*), an aggressive colonizer of the pumice plains at Mt. St. Helens (del Moral and Lacher 2005), has conspicuously villous or pubescent surfaces (Pojar and MacKinnon 1994), which may reduce evapotranspirative stress. Many plants, including disturbance obligates, express greater levels of anthocyanins when presented with physiological stressors such as UV-B radiation and cold (Chalker-Scott 1999). For example, vine maple (*Acer circinatum*) and Oregon-grape (*Mahonia nervosa*), when open-grown, display heightened expression of protective pigments to reduce damage from full sun. Since many disturbances volatilize or liberate nitrogen from organic pools, plants with nitrogen-fixing symbionts may have a competitive advantage. Examples from the Pacific Northwest include the alders (*Alnus*; Harrington 1990), buckbrush (*Ceanothus*; Spears et al. 2001), and even some mosses (e.g., *Funaria hygrometrica*; Scheirer and Brasell 1984).

Many species associated with early seral forest have advantageous dispersal mechanisms for dealing with long colonization distances. For example, whitebark pine (*Pinus albicaulis*) has nutritious, energy rich seeds that induce animal dispersal, especially by the Clark's nutcracker. This endows it with an advantage in high-severity burns of large extent at high elevation (Arno and Fiedler 2005).

Examples of adaptations of early seral organisms are given in Table 1.

Table 1. Adaptations to early seral environments.

Species or Taxonomic Group	*Adaptation*
Willow family (Salicaceae)	Light seeds Vegetative sprouting (from water-dispersed live branches or surviving rootstocks)

Many sclerophyllous shrubs	Resprouting from lignotubers or root systems (*important for reburn events, eg., Donato et al. 2009*)
Forbs/herbs, including members of willowherb (Onagraceae), composite (Asteraceae) families	Light seeds, often with hairs or wings High seed production (example of r-selection)
Maple family	Winged seeds
Buckbrush (genus *Ceanothus*)	Long-lived seeds
Whitebark pine (*Pinus albicaulis*, many other conifers	Animal dispersal to seed caches by birds and mammals (often rodents) to maximize competitiveness with wind-dispersed taxa
Birds, mammals (e.g., deer, bear)	Seasonal migration or normal movements aid in locating newly created early seral habitat
Early seral shrubs (e.g., *Ceanothus*)	Waxy cuticle to reduce desiccation
Early seral herbs (e.g., *Lupinus lepidus*)	Pubescence on stem and leaves to reduce cold/heat/desiccation damage.

Does size matter? What benefits are derived from small patches (<3 acres)?

Disturbances of greater spatial extent cover a wider range of edaphic and topographic conditions, engendering diverse recovery pathways in ways a smaller opening could not. Turner and Dale (1998) emphasize that large disturbances have persistent effects on ecosystems, present tremendous internal heterogeneity due to both stochastic disturbance processes and diversity of recovery pathways, and often host early successional species that can colonize ahead of recovering later-successional species. Large disturbance events interact with a broad geophysical template in diverse ways, creating a variety of spatial patterns and living or dead legacies (Foster et al. 1998). Bailey and Poulton (1968) found a number of seral community types across the extensive Tillamook Burn complex in northwest Oregon; soil moisture availability (a function of topography) and soil texture (a geological and topographical factor) were major determinants of community composition. This has consequences for organisms, such as black-tailed deer, that exhibit seasonal preferences among early seral cover types (Miller 1970). Bunnell (1995) found that wildlife species that are favored by early successional conditions were favored by higher frequency of disturbance (hence a greater proportion of the landscape in early succession) and by larger disturbance extents. Large disturbances may be a factor in the persistence of some tree species; a key example is whitebark pine, which produces valuable seeds for birds, rodents, and the federally-listed grizzly bear.

Small disturbances are more easily colonized by more rapidly growing conifer associates of whitebark pine such as Engelmann spruce (*Picea engelmanni*), while large disturbances confer a spatial advantage on the bird- and rodent-dispersed whitebark pine (Arno and Fiedler 2005).

Smaller disturbance patches tend to fill in more rapidly, since dispersing plant propagules (especially from trees) can access most or all of the disturbed area, decreasing time to recovery (Foster et al. 1998). Furthermore, small patches are generally still under the microclimatic control of the adjacent forest, and experience an array of biotic and abiotic edge effects. However, they may still generate substantial ecological benefits associated with early seral habitats. Hagar (2007) indicates the need to conserve non-conifer vegetation in forest understories, including in gaps across a broad range of sizes. Maintenance of areas of low tree density in young plantations may promote persistence of shrubs into later seral stages. Gaps, along with “wolf trees” and surviving legacy trees, are among the features that predict areas of high epiphyte diversity in young conifer stands in Oregon (Neitlich and McCune 1997).

Van Pelt and Franklin (1999) found a diversity of trees, shrubs, and forbs colonizing gaps in the south Washington Cascades, along with spatial heterogeneity in composition throughout even gaps of modest size (~1 ha). These gaps, however, did not have a high proportion of early seral vegetation, including the seral dominant *Pseudotsuga menziesii*. Gitzen and West (2002) observed an increase in small forest mammals in 1-2 ha experimental gaps, but found that small mammal species characteristic of early succession did not in general respond.

In general, thinning and gap creation are important for revitalizing or initiating understory development (Bailey and Tappeiner 1998, Chan et al. 2006) and creating certain types of wildlife habitat (Hayes et al. 1997), especially when accomplished in a spatially variable manner (Carey 2003). However, for many processes and organisms, these activities do not substitute for the physical and biological changes engendered by a large disturbance that creates a spatially heterogeneous template for ecosystem development.

What impacts does management have on early-seral habitat?

Spies and Johnson (2007) point out that naturally-structured early seral habitat is not well provided for in current land management policy regimes, with far-reaching impacts on biodiversity. The impacts of management on early seral habitat belong to three general forms: 1) changes in disturbance regimes that generate early seral habitats, 2) alterations of structure, composition, or developmental pathways in extant early seral habitat, and 3) changes to pre-disturbance forest (at stand and landscape scales) that result in different structures or developmental pathways following disturbance.

Suppression of fire has led to losses of openings of many sizes in the forests of the Pacific Northwest, especially forests of the interior (Agee 1998, Hessburg et al. 2005). Windthrow events can be enhanced by forest landscape fragmentation (Franklin and Forman 1987, Sinton et al.

2000), but reductions in the proportion of late successional forest in a landscape can result in lower levels of large-diameter woody legacies in post-windthrow environments.

The early seral habitat produced by clearcutting is highly variable in its resemblance to naturally occurring early seral conditions. Woody debris and snags in clearcuts is frequently less abundant than in legacy-rich forest (Pedlar et al. 2002), with attendant consequences for wildlife. Clearcutting can recreate some of the natural processes associated with fire, but is not a functional substitute with regard to many ecosystem attributes (Means et al. 1996). When timber harvest is accomplished, retention of live and dead structures can benefit wildlife (Sullivan et al. 2008,), mycorrhizal fungi (Cline et al. 2005), insect communities (Halaj et al. 2008), diverse plant understories (North et al. 1996) and other ecosystem values. Sullivan et al. (2008) found that seed-tree retention greatly enhanced populations of the northwest chipmunk, an early successional rodent. However, even retention approaches may not provide the functionality of naturally-created early seral habitats. Robertson and Hutto (2007) found that olive-sided flycatcher nesting success was lower in selectively harvested forest than in naturally burned areas.

Salvage logging can result in reductions in available habitat structure, increased erosion, and other negative effects (Lindenmayer and Noss 2006, Lindenmayer et al. 2008). Salvage, especially when followed by dense replanting of conifers, can substantially curtail the early seral phase. Perhaps the best example is presented by salvaged and replanted areas in the blast zone of Mt. St. Helens, where prompt canopy closure by planted Douglas-fir and noble fir resulted in accelerated reduction in non-tree vegetation compared to the adjacent National Volcanic Monument (Titus and Householder 2007). In a very substantial review, Russell et al. (2006) found that salvage logging tends to reduce snag longevity. Bailey and Poulton (1968) note substantial impacts from salvage, including persistent bare soil and increased cover from weedy species such as *Crepis capillaris*, where tractor logging methods were employed. Kotliar et al. (2002) conclude that the effects of fire are specific with regard to various feeding or nesting guilds of birds, and that salvage activities can reduce the abundance and nesting success of birds. When salvage logging is employed in areas where biodiversity conservation is employed, the principles of variable retention should be employed to permit the persistence of some structure (Eklund et al. 2009), especially focusing on retention of large-diameter trees or snags (Beschta et al. 2004).

Compositional simplification of young stands via pre-commercial thinning and herbicide application can reduce or eliminate ecologically important processes. Nitrogen fixation by early seral vegetation such as *Ceanothus* or *Alnus* is an example of a process that may be reduced by compositional simplification of young stands and truncation of the early seral period (Hansen et al. 1991). Kennedy and Spies (2005) found that hardwood-dominated patches in the Oregon Coast Range declined as a landscape element, especially on federal ownerships (lack of harvest or other disturbance) and on private forestlands (intensive conifer plantation establishment).

Intensive management for timber production generally involves rotations much shorter than the historical fire return interval in stand replacing systems, meaning that few trees will live long enough to generate very large snags and down woody debris to enrich post-disturbance systems (Spies et al. 1988, Maser et al. 1988). This is echoed by findings in other regions (Duvall and Grigal 1999).

Invasive plants must be contended with in a number of systems. Compagnoni and Halpern (2011), working in the central Cascades of Oregon, found that exotic vascular plants are ephemeral and weak invaders in Cascadian clearcuts. At low elevations and in proximity to developed areas, invasive plants such as Scotch broom (*Cytisus scoparius*) have the potential to greatly reduce diversity and function (Tveten and Fonda 1999, Keeley 2006).

Conclusions

While the public is not necessarily predisposed against early seral forest (and in some cases may favor certain types), there is still greater public concern over late-successional types (Enck and Odato 2008), likely due to widespread policy and media emphasis on old-growth forests and their relationship to management. However, specific values associated with early seral habitats, from big game production to huckleberry harvesting, are attracting increasing attention from the public. Managers concerned about maintaining rare species are increasingly acknowledging the value of early seral habitats for a substantial portion of the biodiversity of the Pacific Northwest. Potential management responses may include:

- Deferring salvage and dense replanting across all or parts of major disturbed areas (Lindenmayer and Noss 2006, Lindemayer et al. 2008))
- When salvaging, practice variable retention to retain significant structural elements such as large-diameter live trees, snags, and down woody debris (Franklin et al. 1997, Eklund et al. 2009).
- Avoiding reseeding with exotic plant species such as perennial ryegrass (*Lolium perenne*) following fire or volcanic eruption (see Dale et al. 2005b).
- Attempt to incorporate elements of natural disturbance regimes into landcape-scale management (Lindenmayer and Franklin 2002)
- Deliberate creation of large, early seral areas via silviculture (Swanson 2010).

Researchers have an important role to play in facilitating changing attitudes. Much of the excellent research done on seral dynamics in Northwestern forests (e.g., Ruggiero et al. 1991) was focused on biota associated with young, dense forests, mature forests, and late-seral forests. The pre-canopy closure stage component of succession was either not measured (as in Ruggiero et al.), or clumped together with stem exclusion (sensu Oliver and Larson) stands in analysis. While there is an increasing amount of research on true early seral forest, and management responses to these advances (King et al. 2011), much remains to be done in most temperate forest regions both in terms of research and management (Swanson et al. 2011b). It is hoped that the diversity and value of early seral conditions, from clearcuts to structurally and compositionally complex early seral habitat, will come to be recognized and widely incorporated into contemporary land management.

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