Early Seral in Moist Forests of the Pacific Northwest

A synthesis of current science on the response of plant functional groups following retention harvest and natural fire disturbance

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Abstract

This Early Seral Synthesis reviews the research literature on the response of plant functional groups to anthropogenic and natural disturbances in the moist coniferous forests of the Pacific Northwest. For this review, anthropogenic disturbance refers to regeneration harvest, and specifically retention silvicultural systems. The primary natural disturbance in our study region is fire. Federal forest managers in this region recognize the value of early seral habitat and current guidelines provide opportunities for creating conditions conducive to early seral habitat development through retention silvicultural systems. Therefore, the purpose of this review is to inform and assist forest managers in these efforts. This synthesis was produced under contract by the Northwest Oregon Ecology Group, which is comprised of representatives from the USDA Forest Service and USDI Bureau of Land Management in northwestern and coastal Oregon. The synthesis consists of this review and an annotated bibliography.

Variable retention harvest, coarse woody debris, and understory 20 years post-harvest. USFS DEMO Study site

Contents

Acronyms

BLM	USDI Bureau of Land Management
DEMO	Demonstration of Management Options Study
ESH	early seral herbs
ESS	early seral shrubs
FGH	forest generalist herbs (also forest herbs)
FSS	forest generalist shrubs (also forest shrubs)
HJA	H.J. Andrews Experimental Forest
LSH	late seral herbs
PNW	Pacific Northwest
TPA	trees per acre
TPH	trees per hectare
USFS	USDA Forest Service
VRH	variable retention harvest

All photos by Scott Harris unless noted.

Introduction

Following the federal listing the Spotted Owl as a threatened species and the subsequent Northwest Forest Management Plan, federal forest managers in the Pacific Northwest focused on the conservation and creation of late seral forest conditions (Thomas et al. 2006). Since that time, the concept of ecological forestry and ecologically sustainable forest management have gained momentum as a means of addressing the challenge of multiple management objectives. The ecological values provided by early seral habitat are an important component of this trend, and the early seral stage of forest succession has received recent attention by researchers, managers, and policy-makers. In an often-cited review of "the forgotten stage of forest succession", Swanson et al. (2011) describe how early seral forest habitat can contribute to higher levels of biodiversity and ecosystem services across the landscape. Early seral also provides habitat for species not found in other forest successional stages. While the traditional models of forest stand development (e.g. see Oliver and Larson 1996) are useful as a coarse approach to understanding succession, recent research has refined these models to emphasize the multiple alternative pathways of plant succession and vegetation dynamics following disturbance, and the key variables that influence those pathways (Franklin et al. 2002, Donato et al. 2012, Tepley et al. 2013, Reilly and Spies 2015).

Forest management has a significant influence on stand structural and plant community development. Regeneration harvest sets the stage for the development of early seral habitat. Guidelines for federal forest management in our region provide options for different levels and patterns of structural retention and site preparation, which are important factors affecting the trajectory and duration of early seral conditions (USDA Forest Service 1994). The Bureau of Land Management (BLM) in our region specifies that the creation of "complex early successional ecosystems" be a specific objective of regeneration harvest (USDI Bureau of Land Management 2016). This relatively recent interest in early seral combined with a past focus on late successional ecosystems has created the need for this synthesis.

The purpose of this synthesis is to aid our understanding of how variable retention harvest (VRH), a type of retention harvest, can create conditions conducive to the development of early seral habitat and how conditions following VRH compare with conditions following fire. The primary audience for this synthesis is forest managers tasked with incorporating early seral habitat in forest planning. This synthesis reviews the current state of knowledge about the long-term response of plant functional groups to VRH, and compares these responses to those following natural disturbance. Critical questions this synthesis will address include:

1. How do the responses of plants following VRH compare to early seral conditions following clearcut harvest and natural fire disturbance?
2. How do levels and patterns of retention influence plant responses?
3. How does site preparation (slash management, burning, plantings) influence plant responses?
4. What are the key environmental variables that influence the successional pathway following VRH?
5. What is the duration of early seral?
6. What are the primary gaps in our knowledge?

In 2012, Mark Swanson completed a review of the literature on early seral habitat for the Northwest Oregon Ecology Group (Swanson 2012). The Swanson Synthesis is an ideal foundation for this review as it provides a theoretical and conceptual context for early seral forest habitat, an extensive review of natural disturbance regimes, a discussion of the historical abundance of early seral habitat in the Pacific

Northwest, and descriptions of early seral associated taxa. This current synthesis differs from Swanson's in that it focuses more specifically on 1) plant functional group responses, 2) reviews additional empirical studies completed after 2012 (both published and non-published) and 3) has a smaller geographical scope.

Study Region

The forests under the purview of the Northwest Oregon Ecology Group include federal lands west of the crest of the Cascade Mountains and north of the Klamath Mountains in Oregon. They include the Mt. Hood, Willamette, and Siuslaw National Forests and BLM forest lands in northwest and coastal Oregon. For this synthesis, in order to include pertinent empirical studies from similar forest ecoregions, we have expanded the geographical scope to include all forests west of the Cascade crest in Washington and northwest Oregon, as shown in Figure 1. Our geographical scope primarily encompasses the *Tsuga heterophylla* (western hemlock) forested zone, but also includes the *Picea sitchensis* (Sitka spruce), *Abies amabilis* (Pacific silver fir) and *Tsuga mertensiana* (mountain hemlock) zones (Franklin and Dyrness 1973). Zones are named according to the potential climax tree species. The Sitka spruce zone occupies a narrow strip of forest along the Oregon and Washington coasts. The western hemlock zone is an extensive region that includes coniferous forests west of the Cascade crest, the Oregon Coast Range, and the Olympic Peninsula, and is dominated by *Pseudotsuga menziesii* (Douglas-fir)[1]. The Pacific silver fir and mountain hemlock zones are sub-alpine forested areas in the Cascade and Olympic Mountains above 1,000 meters elevation.

Organization of this Synthesis

This synthesis first reviews some of the theoretical foundations and mechanisms of vegetation dynamics following disturbance, from which we develop a conceptual model of early seral. We also describe a gradient in early seral habitat from "simple" to "complex". After describing the management context for early seral in our study region, we then use these basic models to set the stage for the bulk of this synthesis. In each section, we review the important empirical studies in our study region. We discuss management actions and environmental factors that a forest manager should consider when trying to incorporate early seral in harvest planning. These factors include:

- Pre-disturbance plant community
- Level and pattern of disturbance (including retention and slash)
- Overstory tree establishment and canopy closure
- Understory plant community development
- Seed banks and plant propagules
- Landscape context
- Climate and environment

We rely upon empirical studies and quantitative information within our geographical scope as much as possible. When those are not available, we will review studies from similar nearby regions and the important theoretical concepts.

1. The appendix lists the scientific and common names of many plant species in the study region. Hereafter, we will use common names for major coniferous species and use scientifc names for all other species.

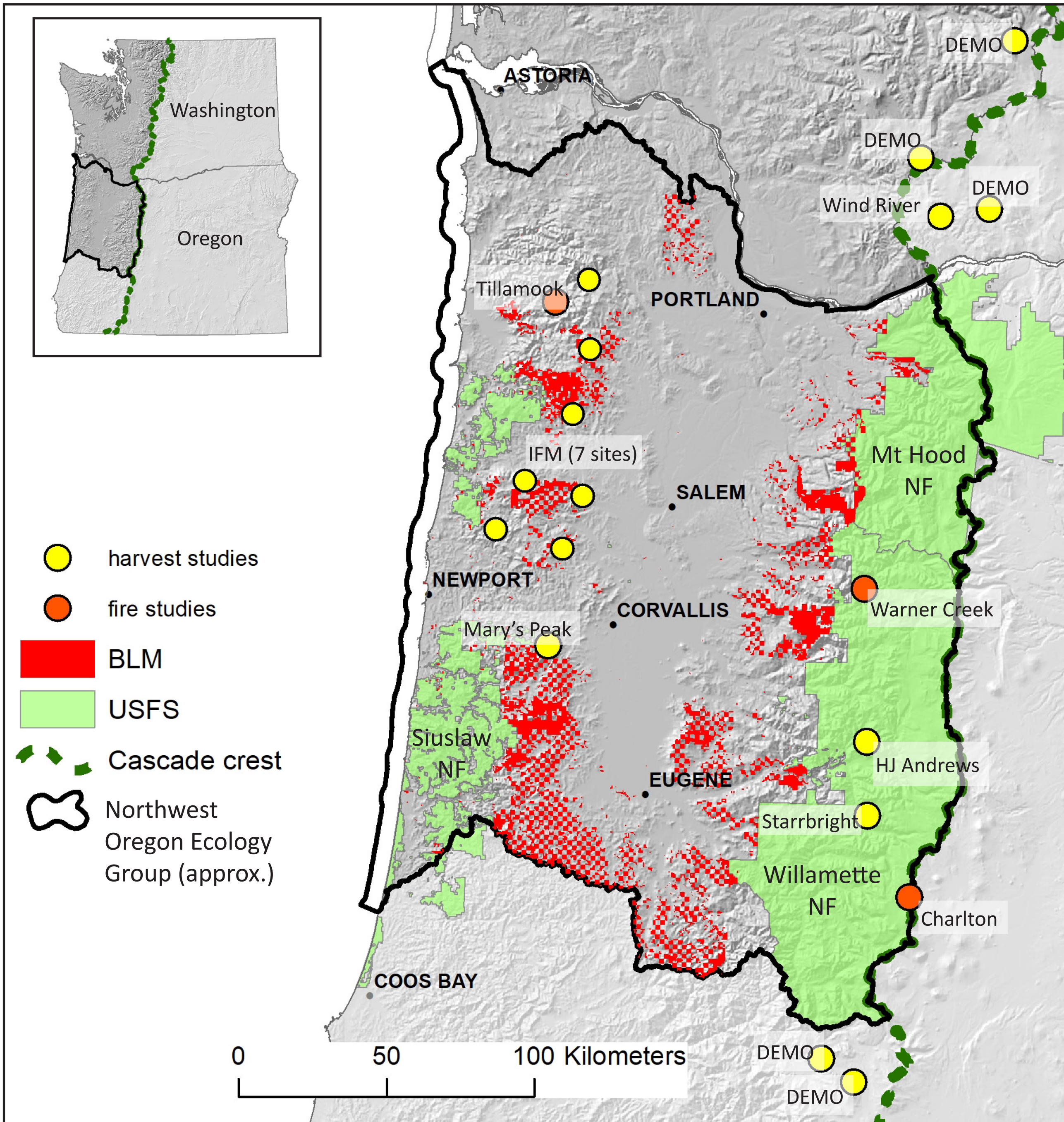


Figure 1. Map showing the US Forest Service and BLM lands under the purview of the Northwest Oregon Ecology Group and the location of the most pertinent studies reviewed for this sythesis. The geogaphical scope of this synthesis includes additional forested lands west of the Cascade crest.

Early Seral - Theory and Management Context

Vegetation Dynamics Following Disturbance

The foundational theories for plant succession and vegetation dynamics following disturbance are rooted in community ecology. From studies of the vegetation dynamics following abandonment of old fields, Egler (1954) described an early conceptual model in terms of relay and initial floristics. Relay floristics describe how species or species groups invade new sites at discrete points in time, maintain dominance for a while, then set the stage for the next invader as they slowly decline. In contrast, initial floristics posit that the pre-distubance plant community plays a key role in subsequent vegetation dynamics. Species may decline or increase in abundance due to community processes, but they continue to persist. Studies that we review in this document more closely follow the initial floristics model. There is ample evidence that the composition of the post-harvest and post-fire plant communities are very similar to the plant communities prior to disturbance. Residual and late seral species may decline dramatically in abundance, but they persist at low levels and slowly regain relative dominance.

Connell and Slatyer (1977) refined Egler's description of the initial and relay floristics models by suggesting the mechanisms that drive vegetation dynamics following disturbance: facilitation, tolerance, and inhibition. Facilitation is the mechanism by which early successional species colonize a newly disturbed site and modify the environment for subsequent later successional species to successfully colonize. An example from early seral would be colonizing shrubs or herbs that modify the microclimate for the successful germination of more shade tolerant species. Inhibition is the mechanism that describes how dominant species suppress the growth or establishment of additional colonists or the additional growth of species already present. Tolerance is the mechanism at the midpoint between the first two, where species present at a site neither inhibit nor facilitate additional colonists and subsequent succession is determined more by the life history traits of individual species.

Metacommunity theory offers additional insight into the processes that drive vegetation dynamics following disturbance (Leibold et al. 2004). A metacommunity is an integrated set of interacting communities that are linked by the dispersal of interacting species (Gilpin and Hanski 1991). Even though the disturbance of harvest is still considered secondary succession, the dramatic change in environmental conditions (e.g. light, micro-climate, soil scarification) at scales delineated by a very discrete edge (the stand) sets the stage for source-sink dynamics where colonists (via seed dispersal) potentially arrive from neighboring communities. The potential for intact forest patches to provide a "lifeboating" function, or a "rescue effect" for the preservation of late seral species at larger spatial scales is also a concept of metacommunity theory. Metacommunity theory is also applicable for considering plant interactions in a hierarchical scale: microsites and individual plants to local communities to the metacommunity of multiple communities within a region.

Environmental filtering has also been suggested as one of the conceptual metaphors for explaining the mechanisms driving plant community assembly. However, Kraft et al. (2015) suggest that while this concept has value, it is widely misused in the research literature. They argue that the environmental filter metaphor is often confounded with biotic interactions. They suggest that the environmental filter metaphor only be used to describe when "an inability to tolerate abiotic conditions leads to the failure of a species to establish and persist at a site". Therefore, an environmental filter can only be tested in the absence of biotic controls such as species interactions. In a meta analysis of 258 published articles that described environmental filtering, they found that only 15% met their narrower definition. Most studies, especially for plants, described plant abundance and diversity along environmental gradients. Because these observed gradients involve species interactions (a biotic process), they are not candidates for consideration by the environmental filtering metaphor, *sensu stricto*.

Theoretical approaches that involve multiple interacting factors best explain the results of the empirical studies we reviewed. Walker and Chapin (1987) and Pickett and McDonnell (1989) further refined the concepts originally proposed by Egler to develop such a multi-factorial interactive model. We have modified their concepts to be more specific to our study of early seral forest systems, which we present in Figure 2. In this model the pre-disturbance plant community sets the stage for future vegetation dynamics. The pre-disturbance community has already been influenced by the topoedaphic and environmental constraints of a particular site. Disturbance is an abrupt change in environmental conditions and the variability in disturbance influences the relative dominance of colonizing species and species from the pre-disturbance community. Subsequent vegetation dynamics are primarily dictated by the life history characteristics of individual species (e.g. reproductive strategies) and their interactions. Examples of facilitation that have been suggested in the literature include ruderal shrubs providing shade to mediate soil moisture and temperature extremes for the germination of more drought-intolerant and shade-tolerant species. Examples of inhibition include the potential effect of recalcitrant leaf litter limiting germination and intraspecific competition for soil resources (Compagnoni and Halpern 2009). Landscape influences on stand-level vegetation include providing sources of seed, pollinators, and vagile herbivores. Climate affects such as drought, frost, and heat affect the performance of individual plant species to germinate and reproduce. In the absence of subsequent disturbance, the plant community typically returns to pre-disturbance conditions.

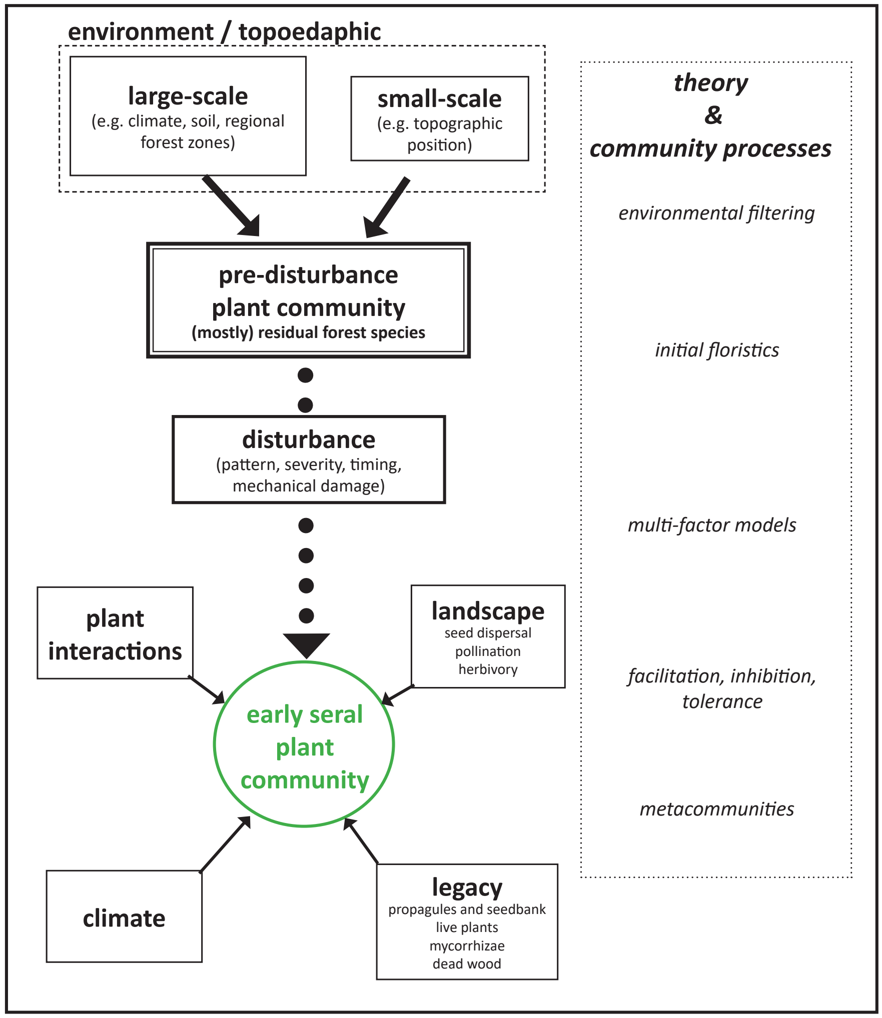


Figure 2. A conceptual model of the processes that affect the post-disturbance vegetation dynamics of early-seral forest plant communities, modified from and incorporating elements of the multi-factorial models of successional change from Walker and Chapin (1987) and Pickett and McDonnell (1989). Theories are described in the text.

Early Seral

Early seral is the successional stage in a forest ecosystem between the time of stand-replacing disturbance and the establishment of a closed canopy (Swanson et al. 2012). While this description is acceptable as a working definition of early seral for this review, it is important to point out that early seral values can persist in forest stands post-canopy closure, and that some post-disturbance successional pathways may lead to delayed canopy closure or none at all. Other terms in the literature for early seral include "early successional" and "pre-forest". The most salient feature of early seral is that while trees are not the dominant plant life form they eventually will be (Franklin et al. 2018).

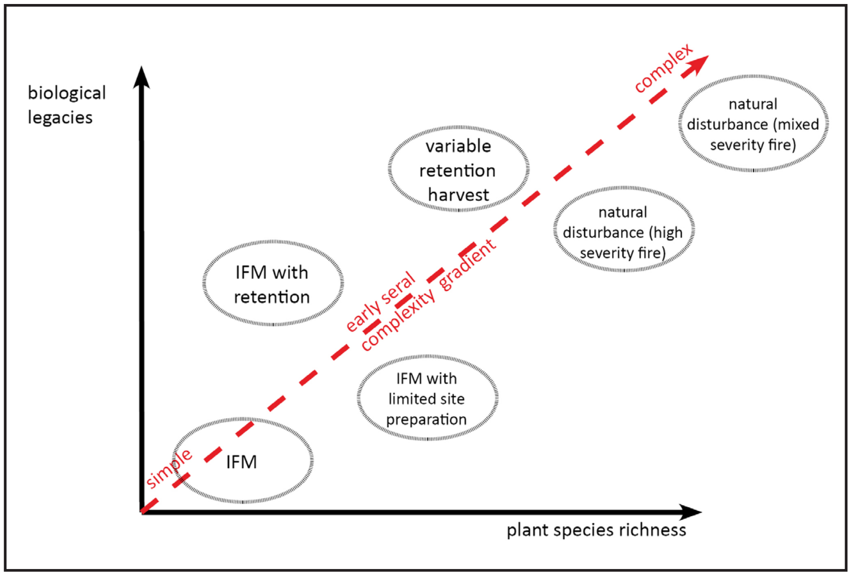


Figure 3. A conceptual model showing a gradient of complexity of early seral forest, with examples of anthropogenic and natural disturbances and generally where they lie along the gradient. IFM refers to intensive forest management as it is practiced on private forest lands in our study area. Biological legacies include both live and dead trees and other plant material retained upon harvest.

There has been considerable debate about the duration of the early seral stage under different management regimes and natural conditions, as well as the specific components that comprise early seral. However, there is general agreement that early seral spans a gradient from simple to complex as shown in Figure 3. The relative contributions of both early and complex seral to biodiversity conservation and timber production is still poorly understood because few studies have independently covaried plant species richness and legacy structures in experimental studies (Betts et al. 2013)

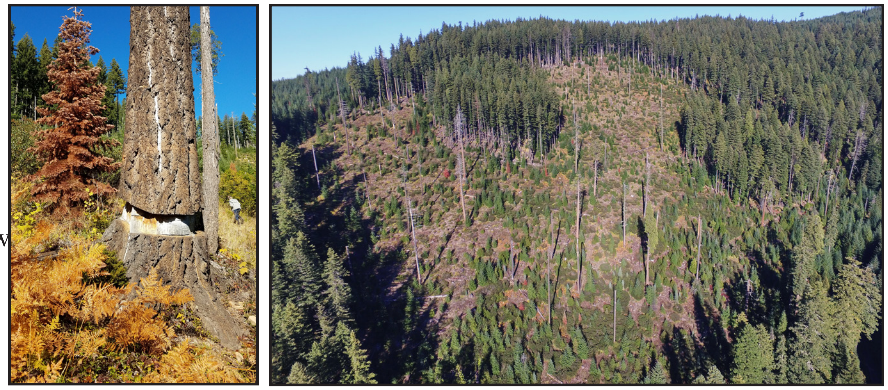
In the moist forests of the Pacific Northwest, forest management on private lands, often called intensive forest management (IFM), creates simplified early seral conditions by reducing the number of biological legacies and conducting extensive site preparation in the form of slash management, broadcast burning, controlling competing vegetation with herbicides, and planting of monoculture crops of primarily Douglas-fir (Hansen et al. 1991, Spies et al. 2002). Complex early seral is typically initiated by natural or stochastic disturbance, such as fire or wind, at multiple scales, levels of severity, and frequency. Complex early seral often results in higher species and structural diversity that incorporates complex ecosystem processes. Forest management on federal lands falls between the two ends of the spectrum by retaining more biological legacies post-harvest and limiting site preparation. These federal harvest practices lead to conditions that more closely resemble the complex early seral following natural disturbance. How closely they resemble natural conditions is the focus of this synthesis.

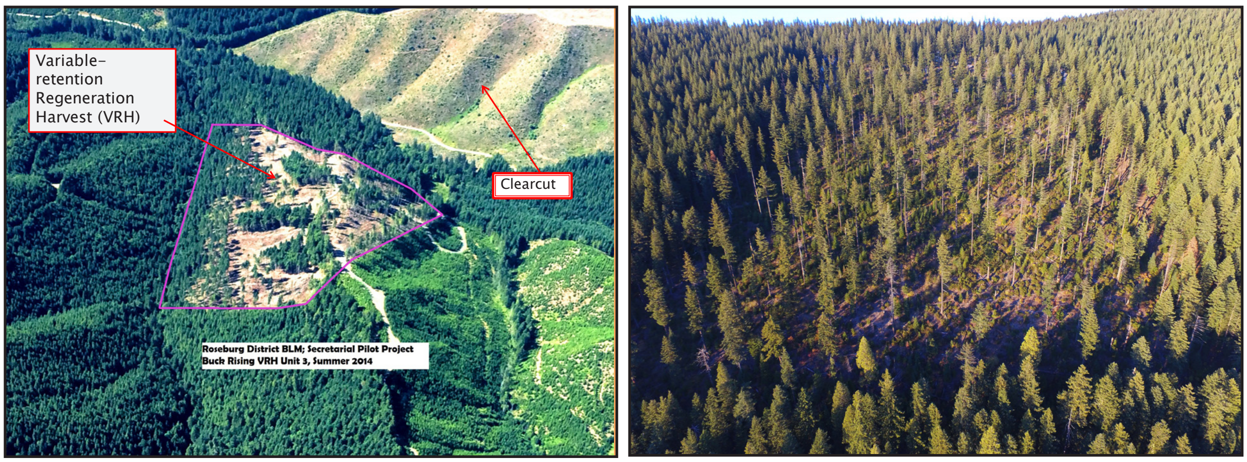
Retention Forestry

Manipulating overstory structure during harvest is one of the primary tool for managers to influence stand development trajectory and the long-term response of plants (Franklin et al. 1997). Retention forestry is defined as (Lindenmayer et al. 2012):

> *An approach to forest management based on the long-term retention of structures and organisms, such as live and dead trees and small areas of intact forest, at the time of harvest. These structures and organisms are not removed in future forest management operations and hence undergo natural processes of growth and decay. The aim is to achieve a significant level of continuity in forest structure, composition, and complexity*

Figure 4. Examples of retention harvest. Clockwise from right: Created snag via girdling. 15% retention in 1 hectare aggregates. 15% dispersed retention. The first 3 photos are from the USFS DEMO study, Watson Falls site, 20 years post-harvest. Photo below is a BLM harvest in the Roseburg District, compared to a clearcut (BLM *photo of courtesy Douglas Forest Protective Association*).





> *that promotes maintenance of biodiversity and ecological functions at different spatial scales. Approaches and levels of retention, which take account of natural disturbance dynamics, differ depending on local context but the practice is appropriate for all types of silvicultural systems and forests.*

Retention forestry, of which variable retention harvest (VRH) is one example, utilizes multiple alternative options to achieve management objectives: amount of retention, type of structures retained, pattern of retention, and timing of harvest. Lindenmayer et al. (2012) concluded that retention forestry can meet dual conservation and timber production objectives and Baker et al. (2016) reported that retention forestry with these objectives is already being applied across the globe.

From these descriptions, it is apparent that the renewed interest in retention forestry has been focused on providing for a continuity in forest stand conditions from pre-harvest to late seral, and in the potential of retention harvest to maintain late seral species through a “lifeboating” function (Franklin et al. 1997). In a meta-analysis of retention harvest studies, Rosenvald and Lohmus (2008) noted that most recent retention harvest studies were focused on this “lifeboating” concept. In contrast, the potential of retention harvest for creating early seral conditions has been poorly studied.

Recognizing the importance of retention in influencing post-harvest stand development, the USFS, BLM, and Oregon Department of Forestry include structural retention in their harvest guidelines. Table 1 lists the general management guidelines for timber harvest in Oregon by land management agency. There are additional details, particularly for harvest on private lands, that are not fully described in Table 1. Figure

4 shows examples of retention practices on federal lands in our study region.

The Demonstration of Ecosystem Management Options (DEMO) study in Washington and Oregon (Figure 4). was specifically designed to experimentally test the influence of pattern and amount of retention on ecological responses following harvest (Aubry et al. 2009). The study design includes six treatments: 75% aggregated retention, 40% aggregated retention, 40% dispersed retention, 15% aggregated retention, 15% dispersed retention, and an unharvested control (100% retention). Aggregates are 1 hectare circular patches. DEMO is the only study in our region that measures the understory response of plants following retention harvest at these levels and patterns. Even though DEMO was designed within the context of the Northwest Forest Plan and the emphasis on "lifeboating" and creating late seral conditions, results of this study provide valuable insights into early seral conditions following retention harvest.

Agency	Current planning document	Land designation	Retention	Snags	Coarse woody debris (downed wood)
USDI Bureau of Land Management, Northwest and coastal Oregon	Northwestern and Coastal Oregon Resource Management Plan (2016)	Harvest Land Base	Retain 5 – 30% pre-harvest basal area (live trees) in aggregates and dispersed patterns	Retain >20" dbh and other sizes as prescribed. Includes snag creation to meet minimum standards	
USDA Forest Service	Northwest Forest Plan (1994)	Matrix[1]	Retain 15% of pre-harvest basal area[2]. 70% of retained area in aggregates of 0.2 to 1 hectare	Retain snags at levels to support species-specific population models[3]	>= 240 linear feet of logs per acre >= 20" dia, logs must be >= 20 feet long[4]
USDA Forest Service	Northwest Forest Plan (1994)	Late Successional Reserves	N/A	N/A	N/A
Oregon Dept. of Forestry	NW Oregon State Forests Management Plan (2010)	Board of Forestry[5]	District-level and harvest-level planning provide quantitative goals for reten structures, and stand sizes across the landscape, emulating natural pat		
Oregon Dept. of Forestry	Oregon Forest Practices Act	Private forests	Minimum of 2 wildlife trees and 2 logs per acre[6]	Live or dead trees >11" dbh and >= 30' height[6]	> 10 ft^3 gross volume[6]

1. Also an intent guideline for Adaptive Management Area designations
2. Oregon Coast Range and Olympic Peninsula are exempted because other protections in matrix lands meet this minimum requirement
3. Primarily cavity nesters. Also considers bats.
4. Western Oregon and Washington
5. 3% of state lands in NW Oregon are Common School Forest Lands
6. The Oregon Forest Practices Act has more specific standards that are dependent upon harvest size and site class. Also, combinations of of tree sizes and densities can meet required retention.
7. Requirements vary depending upon site class. Combinations of different tree sizes can meet minimum standards.

Table 1. Management guidelines for forested lands in the study area, showing the options for structural retention and site preparation.

Review of Empirical Studies

Tree Regeneration and the Duration of Early Seral

A significant factor affecting understory vegetation dynamics and the duration of early seral habitat conditions is the structural development of the regenerating cohort of trees. High stocking densities of conifers, whether from planting or natural regeneration, truncates the early seral stage and leads to more simple early seral conditions (see Figure 3). Overstory canopy closure causes changes in the light and microclimatic conditions for the understory plant community. Even without full canopy closure, overstory trees will effect the understory plant community through other processes such as resource competition (Franklin et al. 2002, Donato et al. 2012, Halpern and Lutz 2013). However, Halpern and Lutz (2013) injected a critical caveat into the assumption that canopy closure exerts strong controls over understory vegetation dynamics. They found that while overstory structure changed dramatically over the 45 years following a clearcut harvest (stem density increased by 75%), the understory biomass experienced relatively less change (declines of 30-40%). Using quantile regression models, they found

Salvage harvest	Site preparation	Tree density post-harvest	Tree density post-natural disturbance	Large/old trees	Thinning	Thinning
Retain minimum of 5% or 15% (combination of live and snag) in aggregates and dispersed patterns	Brushing and fire. No herbicides	130 or 150 tpa within 5 years (natural and/or artificial regen)	Reforest to 130 or 150 tpa within 10 years	Retain >40” dbh and over 165 years old	Tree density 25-45% of pre-thin.	5% min area untreated (skips). 10% max area in group openings
	Brushing and fire. No herbicides			In watersheds with <=15% late-seral forests, protect late-seral patches	No specific guidelines	
Only for stand-replacing natural disturbance >10 acres and stands > 80-110 years. Retain all live trees. Downed wood criteria determined by site-specific plans	N/A	N/A	N/A		No thinning in stands >=80 years old	
ention, site preparation, etc. The regional document describes management principles that include providing for a "variety of seral stages, stand patterns" at the landscape scale, and managing for important structural features including snags, down wood, large trees at the stand scale.						
N/A	Brushing, fire, and herbicides	100-200 tpa planted within 2 years and achieve 60-120 tpa within 6 years[7]	N/A	N/A	same retention guidelines as harvest	

Table 1 (continued). Management guidelines for forested lands in the study area.

that understory vegetation dynamics and overstory structural changes were weakly linked.

Tree regeneration is influenced by many factors including; the severity and timing of disturbance, the availability of seed, life-history traits of species, topoedaphic conditions, herbivory, pests, and environmental conditions such as drought, frost, or heat. The following review of the research literature on regeneration density and the duration of the establishment phase following disturbance provides forest managers with guidance for comparing conditions following retention harvest with natural disturbance and clearcut harvest.

Natural and artificial regeneration

Following harvest and site preparation, current practice in our study region is to plant Douglas-fir nursery stock to accelerate the development of production timber stands. Historically, natural regeneration has been shown to be inadequate for commercial forest lands (Brown et al. 2013). Isaac (1938) reported that up to 70% of all naturally regenerated stands following harvest in southwest Washington were inadequately stocked. In his study, first year natural seedlings had mortality between 50 and 80%, with higher survival for seedlings under light shade. By the end of 4 years, only 5% of the first cohort were still alive. Heat was the primary cause of mortality, and seedlings over fire-charred darker soils experienced higher mortality. Isaac concluded that soil temperature was the most important factor affecting Douglas-fir seedling survival. He suggested minimal slash burning, especially on exposed southern aspect slopes.

In another study, Isaac (1940) measured tree and understory cover in 15 areas throughout western Washington and Oregon that were clearcut and subsequently burned. Isaac noted substantial mechanical ground disturbance from harvest activities. He found that naturally regenerated Douglas-fir had the shortest and most productive establishment periods under light shade (up to 25%) that was produced by shrubs and other colonizing species.

Hermann and Chilcote (1965) conducted a manipulative field experiment in the Oregon Coast Range and found that sown Douglas-fir seeds had higher germination success on soils that experienced higher fire severity. They suggested their results differed from Isaac's (1938) due to the different soil conditions at their sites, microclimate, and the higher moisture-holding capacity of charred soils. First year mortality of seedlings was 62%, primarily due to rodents, heat, and fungi. Mortality decreased significantly in subsequent years and Douglas-fir continued to germinate from seed for many years. Mortality was lower under light shade.

Even though Douglas-fir produce large seed crops, seeds are only viable in the soil for approximately one year (Isaac 1935), so evidence for continuous establishment suggests aerial seed sources. Douglas-fir cones start to shed seeds in early September. Most seeds fall before heavy rains start in October when cones close due to moisture. While highly dependent on wind, aerial seed dispersal was experimentally shown to range up to 1/4 mile (Isaac 1943). West and Chilcote (1968) found that the timing of aerial seed dispersal and slash burning strongly determined germination success. They concluded that late summer was the ideal time for a burned soil surface to be available to dispersing Douglas-fir seeds. Larson and Franklin (2005) suggested that rapid and dense establishment of Douglas-fir following the Warner Creek Fire was due to an "aerial seed bank" in the canopy, and that the timing of the fire was ideal for germination. Their results suggest the importance of an on-site seed source in addition to longer-distance aerial dispersal.

Establishment and regeneration density

In our study region, two stand development trajectories following a natural fire disturbance have been described in the literature: a rather rapid establishment period that can be as short as 20 years followed by a canopy closure period, or a protracted establishment period that can last a century or more and possibly never develop a fully closed canopy (Donato et al. 2012).

A study by Tappeiner et al. (1997) supports the protracted establishment model. From measuring growth rings on old growth stumps in coastal Oregon, they concluded that their stands established at very low densities and may have never entered a self-thinning stage. After calibrating a stand development model with field measurements, they estimated stand densities of 77-144 TPH at age 20 years. Poage and Tappeiner (2002) also concluded that post-fire establishment of Douglas-fir was at low densities, based on tree stump measures that showed sustained basal area increments. Poage et al. (2009) reached similar conclusions based on a meta-analysis of tree core and stump studies across 205 old-growth forest sites in Oregon.

However, studies that have directly measured seedling density following fire support the higher-density establishment model. Twenty years following the Hoskins fire in the Oregon Coast Range, Marshall and Curtis (2002) reported Douglas-fir densities of 651-763 TPH. Brown et al. (2013) measured the tree and understory plant response following the 3,631 hectare Warner Creek fire of 1991. This mixed-severity fire burned areas from 700 to 1,800m elevation. They observed abundant natural regeneration that continued for several years. Seedlings 14 years post-fire ranged from 1,530 to 392,000 per hectare.

"Establishment" ≠ "Canopy Closure"

In the literature we reviewed, establishment of a forest stand referred to the period of time when the majority of the individuals in a cohort of trees successfully germinated and became seedlings. The establishment period ends when no more trees germinate in that cohort. The establishment period can also begin as advanced regeneration before a major disturbance. Canopy closure is the process over time that occurs concurrent with and following establishment. The canopy closure stage ends when the overstory tree canopy reaches a subjectively-defined level. Ranges in the literature we reviewed have spanned 70 to 100%. There can be considerable variation in the duration of both the establishment and canopy closure stages. For example, establishment in densely stocked commercial stands can be as short as one year. In our review, we found examples when the duration of the establishment stage was incorrectly equated with the time to canopy closure following disturbance. We suggest that readers of the literature consider the establishment stage as providing insight on the productivity of the stand and to infer the potential duration of the canopy closure stage. See Franklin et al. (2002) for further discussion.

In a study of over 3000 trees ranging in elevation from 253 to 1,753m in the western Cascades of Oregon, Tepley et al. (2014) identified the establishment periods of multiple regenerating cohorts. The multiple cohort approach assumes that each cohort establishes along an independent pathway and time frame. This approach also recognizes the increase in temporal and spatial stochasticity of mixed and patchy fire disturbance regimes. The majority of the cohorts they measured had an establishment period of approximately 40 years. This finding was consistent across elevation, aspect, topographical position, and even the past eight centuries. Eight percent of their cohorts established within 20 years and 12% had an establishment period of greater than 80 years. In the same study area, Tepley et al. (2013) found that Douglas-fir developed single cohorts following stand-replacing fire, and multiple cohorts at lower densities following non stand-replacing fires.

In a coring study of 233 old growth trees in the western Cascades, Winter et al. (2002) found an establishment period of approximately 20 years, comprised mostly of Douglas-fir and some western hemlock. Based on radial growth patterns, they estimated that canopy closure was a gradual process during the 20 years following establishment. In a study of 18 stands in the western Cascades spanning elevations from 318 to 990m, Freund et al. (2014) concluded a mean establishment period of 60 years (95% CI 50-70). From a coring study In the Olympic Mountains, Huff (1995) concluded that establishment of mixed Douglas-fir and western hemlock stands took 35-50 years following stand-replacing fire. Other studies in our region with less replication have shown establishment periods of 75 years or less (Kuiper 1994, Zenner 2005).

How do these findings of density and establishment in natural stands compare with clearcut and retention harvest? Following the clearcut of experimental watersheds in the H.J. Andrews Experimental Forest, Lutz and Halpern (2006) measured 3,000 TPH (approximately 54% Douglas-fir) 22 to 25 years following harvest and slash burning. In the retention harvest DEMO study previously described, Maguire et al. (2006) found that advanced regeneration 6 years following harvest ranged from 33 to 6,545 TPH. This is in addition to post-treatment planting at densities 341 to 604 TPH. They found that planted seedlings experienced 1-14% annualized mortality during the 6 years following treatment.

Yang et al. (2005) compared the successional trajectories of clearcut stands in the western Cascades with the Oregon Coast Range. They found significant variability in the rate of succession based on photo-interpretation of 153 stands in the Siuslaw and Willamette National Forests. To accommodate this variability, they modeled tree cover succession using a Chapman-Richards growth function. They calculated a mean time to 70% canopy closure of 23 years in the Coast Range compared to 42 years in the western Cascades. The rate of succession was nearly twice in the Coast Range. Over 25% of the western Cascades stands they interpreted never reached canopy closure. All the Coast Range stands did reach canopy closure. However, in the Coast Range, 15% of those stands had either mixed or complete dominance by hardwoods. For comparison, only 3% of the western Cascade stands had an important hardwood component. Aerial photos confirmed that the Coast Range stands experienced more hardwood cover than the western Cascades.

Understory Plant Responses

For describing the understory vegetation dynamics following disturbance, we adopt a trait-based approach for classifying plant species into groups. Classifying plants into functional groups reduces taxonomic resolution as well as the ability to assess intraspecific effects on community assembly. However, it has been shown to be effective for predicting future vegetation community changes and for revealing and understanding ecosystem processes (Burton et al. 2012, Diaz et al. 2016, Levine 2016).

All the studies we reviewed classified plant species into functional groups. Unfortunately, there have been no standard categories and many groups were subjectively assigned by the authors. In this review we report the functional groups used for each study. When synthesizing and comparing multiple studies we adopt the functional groups specified by Halpern et al. (2012) for the DEMO study (see Table 5 and the Appendix). These groups are early seral herbs, early seral shrubs, forest generalist herbs, forest generalist shrubs, late seral herbs, bryophytes, trees, and unclassified species. The herb groups include graminoids, ferns, and short shrubs

The Appendix provides a species list with the associated functional group assignments. Additional terms utilized by the literature include: 1) residual species and plant groups refer to plants that are primarily found in undisturbed forests, 2) colonizing species and plant groups, also referred to as invaders, early seral species, and ruderals, refer to plants that are primarily absent from undisturbed forests. Exotic, non-native, and invasive species are considered synonymous in this review.

DEMO is the only retention harvest experiment in our study region. Because of the paucity of information on understory plant responses to retention harvest, we will also review studies following

Site / Study	Study notes	Disturbance	Response measures (years)	In this review	Reference
HJ Andrews	2 watersheds in western Cascades of Oregon	clearcut and slash burning	0-7	Table 4	*Dyrness 1973*
			0-21	Table 3, Figures 6 and 7	*Halpern 1989*
			-4-25	Figure 12	*Halpern and Franklin 1990*
			15-45		*Halpern and Lutz 2013*
Starrbright	Oregon Cascades	clearcut and slash burned	1-16		*Compagnoni and Halpern 2009*
IFM	replicated experimental design in Oregon Coast Range	clearcut and slash burning	1-7	Figure 12	*Stokely et al. in review*
Mary's Peak area	Oregon Coast Range, *Senecio sylvaticus*	clearcut and slash burning	1-10		*West and Chilcote 1968*
DEMO	replicated experimental design across Washington and Oregon	variable retention harvest	0-2	Figures 10, 12 and Table 5	*Halpern et al. 2005*
			0-11		*Halpern et al. 2012*
			1-2		*Nelson and Halpern 2005*
Tillamook	series of fires in Oregon Coast Range	fire	17-29	Table 6 and Figure 12	*Bailey and Poulton 1968*
Warren Creek	Oregon Cascades, high elevation	fire	1-14	Figure 12	*Brown et al. 2013*
	Oregon Cascades, low elevation				
Charlton	Oregon Cascades	fire	1-15		*Acker et al. 2017*

Table 2. Empirical studies within the geographical scope of the NW Oregon Ecology Group that measured understory vegetation dynamics following disturbance.

clearcut harvest. There are only a few post-fire studies. The important empirical studies in our region are shown in Table 2, discussed in the following sections, and compared in Figure 12.

Clearcut harvest

Studies from Watersheds 1 and 3 of the H.J. Andrews Experimental Forest (HJA) are the most thorough examination of vegetation dynamics following clearcut harvest in our study region. These approximately 100-hectare watersheds lie between 440 and 1,100m elevation on the western slope of the Oregon Cascades. Geology is composed of andesites, basalts, tuffs, and breccias that have been subjected to mass movements and resorting typical of the region. The soil has a moderately high moisture holding capacity (Rothacher et al. 1967). Vegetation and environmental conditions are considered typical of moderately productive forests in the western Cascades. The pre-harvest stands were dominated by 125-500 year old Douglas-fir and western hemlock. Rothacher et al. (1967) identified six pre-disturbance vegetation communities described in Table 3 that span a gradient of available moisture. These communities have been used consistently and further refined by subsequent studies.

Watersheds 1 and 3 were clearcut harvested between 1962 and 1966. After aerial seeding failed, regeneration of Douglas-fir consisted of a combination of plantings and natural regeneration (Halpern 1989). Variation in ground disturbance from harvest and variation in slash burning provided the opportunity to study responses to a gradient in disturbance. Dyrness (1973) described plant succession for the first 7 years following harvest (only in Watershed 1). Halpern (1989), Halpern and Franklin (1990) and Halpern and Lutz (2013) followed from Dyrness and described plant succession during the 45 years following harvest. This time period includes vegetation dynamics through canopy closure.

plant community	topoedaphic characteristics and notes	dominant growth form	dominant species
Corylus cornuta - Gaultheria shallon	south-aspect slopes, shallow soils,	tall shrubs	*Corylus cornuta , Acer circinatum , Berberis nervosa*
Rhododendron macrophyllum - Gaultheria shallon	ridgetops, mid-slope benches, sparse tree canopy	tall shrubs, herbs, low shrubs	*Rhododendron macrophyllum, Gaultheria shallon*
Acer circinatum - Gaultheria shallon	south aspect mid to upper slopes, open timber stands	herbs and low shrubs, tall shrubs	*Gaultheria shallon , Acer circinatum*
Acer circinatum - Berberis nervosa	mid to lower slopes, relatively productive conditions for timber	tall shrubs	*Acer circinatum*
Coptis laciniata	mid to lower slopes, dense overstory	understory trees	*Tsuga heterophylla*
Polystichum munitum	north to east aspect, bottom and steep slopes, seeps, productive conditions for timber	herbs and low shrubs, tall shrubs	*Polystichum munitum , Acer circinatum*

decreasing soil moisture

Table 3. Pre-harvest plant communities of HJA Watersheds 1 and 3 as classified by Rothacher et al. (1967). Halpern (1987, 1989) added additional descriptions.

Dyrness (1973) found that while the pre-harvest plant community declined in abundance, it still persisted through the first 6 years following harvest. Species loss during the first six years was 13%. Total plant cover tripled in the first 2 years, mostly from colonizing *Epilobium spp* and *Senecio sylvaticus* (Figure 5). Forest species such as *Rubus ursinus* and *Linnea borealis* also had noteworthy increases. *Senecio sylvaticus* responded rapidly in the first 2 years to 15% mean canopy cover, then rapidly declined.

The dynamics of *Senecio sylvaticus*, an exotic annual herb, deserve special attention. West and Chilcote (1968) reported similar results to Dyrness for this species from a study near Mary's Peak in the Oregon Coast Range. North et al. (1996) found that *Senecio sylvaticus* was the most common species 6 years following clearcut and retention harvested forest sites near Seattle, Washington. Halpern et al. (1997) studied *Senecio sylvaticus* in a manipulative experiment following clearcut at the Starrbright site in the western Cascades of Oregon. They found that *Senecio sylvaticus* germinated on all soil types, but had higher abundance on burned mineral soils. Viable seeds of *Senecio sylvaticus* were shown to be abundant in forest soils in southwest British Columbia (McGee and Feller 1993) and can remain viable for up to 100 years (Harrington 1992). *Senecio* seed is susceptible to heat damage from fire (Clark 1991). The most striking result of the Starrbright study however, was that competition with other colonizing

Figure 5. Some common early seral species colonizing recently disturbed sites. Left to right: the shrub *Ceanothus velutinus* (snowbrush, family *Rhamnaceae*) the herb *Senecio sylvaticus* (woodland groundsel, family *Asteraceae*), and the herb *Epilobium angustifolium* (fireweed, family *Onagraceae*). (*Photos from California Native Plant Society, Oregon State University, Univ. of Maine*)

Disturbance class	Species richness	Important early seral species	Other species and notes
undisturbed - unburned	39	*Ceanothus velutinus, Epilobium spp*	*Acer circinatum, Vaccinium parvifolium, Tsuga heterohphylla, Oxalis oregana, Gaultheria shallon*
disturbed - unburned	56	*Anaphalis margaritacea, and Campanula scouleri.*	many shrub and tree species, especially *Rubus parviflorus* and *Rubus Leucodermis*
disturbed - lightly burned	48	*Epilobium spp, Cirsium vulgare, Gnaphalium microcephalum,* and *Senecio sylvaticus, Ceanothus velutinus*	dominance by early seral species
disturbed - severely burned	24	*Epilobium spp, Cirsium vulgare, Gnaphalium microcephalum,* and *Senecio sylvaticus, Ceanothus velutinus*	dominance by early seral species, very few shrubs and tree species present

Table 4. General plant responses 6 years following clearcut harvest and slash burning in Watershed 1 at the HJ Andrews Experimental Forest in the western Cascades of Oregon. Responses are grouped according to subjectively-assigned disturbance classes that incorporate mechanical distrurbance and burning severity (Dyrness 1973).

or residual species had no effect on the rise and decline in abundance of *Senecio*. The increase, up to 10-fold at Starrbright, was attributed to copious seed production from the few colonizing plants that first arrived on site. . While Halpern et al. (1997) offered several suggestions, the mechanism for the rapid decline in *Senecio* is still unknown.

Dyrness also showed that understory plant responses varied with logging disturbance and burning severity, shown in Table 4. Total plant cover was consistently highest in the undisturbed-unburned plots, dominated by residual forest species that increased their cover following overstory removal: *Acer circinatum, Vaccinium parvifolium, Tsuga heterohphylla, Oxalis oregana,* and *Gaultheria shallon*. High cover species in undisturbed-unburned plots included: *Cornus nuttaflii, Taxis brevifolia, Linnaea borealis, Polystichuiin munitum,* and *Rubus ursinus*. The most important colonizing plants were *Ceanothus velutinus* and *Epilobium angustifolium* (Figure 5). Plant species richness was highest in the disturbed and unburned plots. Disturbed and either lightly or severely burned plots had similar responses of colonizing species but severely burned plots had fewer shrubs and tree species.

Halpern (1989) refined the descriptions of Dyrness (1973) and updated the results to cover 21 years following disturbance. He found that general plant responses over the 21 years were characterized more by gradual changes in abundance and dominance than by abrupt transitions. He explained plant responses as a combination of both deterministic and stochastic mechanisms. Deterministic mechanisms included the disturbance-resistant characteristics and life-history traits of the pre-harvest plant community. Examples include individual species' tolerances to increased light or tolerances to mechanical damage from harvest. Stochastic mechanisms included variation in disturbance (e.g. mechanical disturbance from harvest and slash management). Additional stochastic mechanisms could include environmental stress (e.g. frost and drought). Twenty-one years after slash burning, richness increased 66% and 88% in Watersheds 1 and 3, respectively. Survival of residual species after slash burning was 71% to 82%, and species colonizations occurred mostly in the first 2 years at a rate of 11-19 species/year. Herbs and low shrubs peaked first in terms of canopy cover. Tall shrubs and trees increased more slowly and were at a peak by the last sampling event at approximately 21 years. Halpern (1989) described species-specific responses, and also subjectively assigned species to 11 plant population patterns based on seral stage, timing of peak abundance, magnitude of peak abundance, and duration of elevated abundance. The 6 colonizer groups, which Halpern termed invaders, are shown in Figure 6

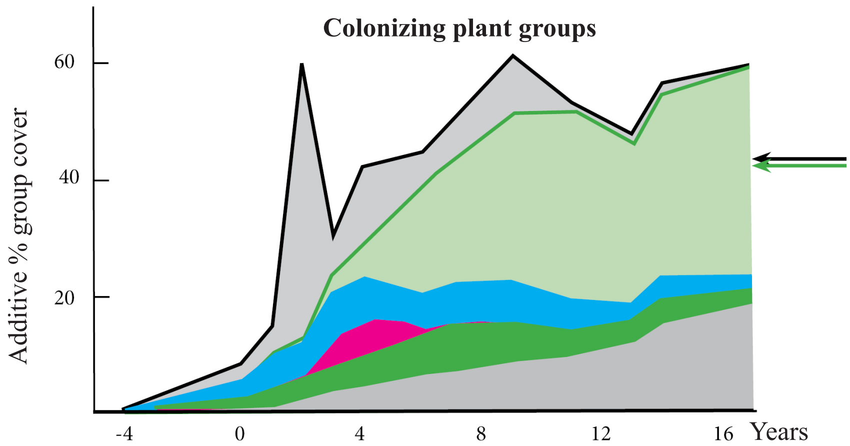


Figure 6. Redrawn from Figure 1 and summarized notes in Halpern (1989). Changes in total additive canopy cover for colonizer ("invader") species groups in HJA Watershed 1. Time -4 is pre-harvest. Time -3 to 0 is the 4-year harvest period. Time 1 is the first growing season following slash burning. Group responses in Watershed 3 were similar except that group I5 declined in canopy cover. That difference is depicted by the arrows at the right side of the graph.There are important species-specific differences between Watersheds 1 and 3 not depicted in this figure. Responses after 16 years (but in different functional groups) for these watersheds can be seen in Figure 12.

symbol	growth form	species	group	notes
(dark grey)	herbs and low shrubs	*Senecio sylvaticus, Epilobium paniculatum, Conyza canadensis*	I1	Annuals. *S. sylvaticus* is non-native. Timing of disturbance and life history of species influence response. Strong response on burned sites.
(light green)	tall shrubs	*Ceanothus velutinus, Ceanothus sanguineus*	I5	Abundance increases with disturbance. Very long-lived seed bank. Different response on Watershed 3 may be due to severe localized frost.
(blue)	herbs and low shrubs	*Epilobium angustifolium*	I2	perennial. Wind-dispered seed supplemented by subsequent vegetative propagation
(pink)	herbs and low shrubs	*Agoseris spp, Cirsium spp, Gnaphalium microcephalum, Lactuca serriola*	I3	Annuals. Biennials, and Perennials. Wind-dispersed seed. *Compositae* family.
(green)	herbs and low shrubs, tall shrubs	*Anaphalis margaritacea, Rubus leucodermis, Collomia heterophylla, Vicia americana, Bromus spp*	I4	Abundance probably attributed to combination of wind- and animal-dispersed seed and vegetation propagation
(light grey)	herbs, low and tall shrubs, trees	*Pteridium aquilinum, Rubus parviflorus, Salix scouleriana, Prunus emarginata*	I6	Perennials. Many seed-dispersal mechanisms but R. parviflorus likely animal-dispersed.

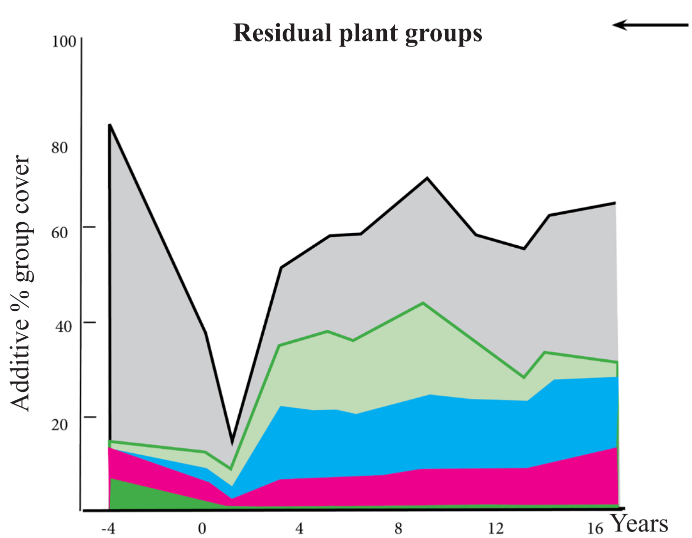


Figure 7. Redrawn from Figure 1 and summarized notes in Halpern (1989). Changes in total additive canopy cover for residual species groups in HJA Watershed 1. Time -4 is pre-harvest. Time -3 to 0 is the 4-year harvest period. Time 1 is the first growing season following slash burning. Relative group responses in Watershed 3 were similar except that group R3 had nearly twice as much canopy cover. That difference is depicted by the arrow at the right side of the graph.There are important species-specific differences between Watersheds 1 and 3 not depicted in this figure. Responses after 16 years (but in different functional groups) for these watersheds can be seen in Figure 12.

symbol	growth form	species	group	notes
(dark grey)	herbs, low and tall shrubs, trees	*Acer circinatum, Polystichum munitum, Gaultheria shallon, Rhododendron macrophyllum, Berberis nervosa, Corylus cornuta, Tsuga heterophylla*	R3	The dominant pre-disturbance species. Most likely regenerated from vegetative propagules
(light green)	herbs and low shrubs	*Trientalis latifolia, Whipplea modesta, Hieracium albiflorum*	R2	All three species have different reproduction strategies and tolerance to disturbance
(blue)	herbs and low shrubs	*Rubus ursinus*	R1	Rapid increase in abundance and dominance seemed independent of disturbance severity.
(pink)	herbs, low and tall shrubs, trees	*Coptis laciniata, Viola sempervirens, Vaccinium parvifolium, Castanopsis chrysophylla, Oxalis oregana, Rubus nivalis, Acer macrophyllum, Cornus nutallii*	R4	Diverse group of with species-specific variability in abundance
(green)	herbs, low shrubs, trees	*Chimaphila umbellata, Thuja plicata, Goodyera oblongifolia, Synthyris reniformis, Taxus brevifolia*	R5	Sensitive to disturbance

and the 5 residual groups are shown in Figure 7. These figures show the plant responses for Watershed 1. The different responses for Watershed 3 are described in the accompanying notes. These figures are useful in that they show the variation in general patterns of early vegetation dynamics following a clearcut disturbance.

Halpern and Franklin (1990) discuss results of the HJA studies in terms of the broad plant functional groups: early seral herbs, early seral shrubs, forest generalist herbs, forest generalist shrubs, and trees. They again reiterate the importance of the pre-disturbance plant community in shaping the rate and relative dominance of functional groups following disturbance. They concluded that from those five groups, the ones most strongly influencing post-disturbance vegetation dynamics were residual forest herbs, early seral shrubs, and trees. Early seral herbs played a significant role on some sites but only very early and declined rapidly (e.g. *Senecio sylvaticus*). For both HJA watersheds, forest residual herbs were the dominant (by canopy cover) functional group for much of the early seral stage, regardless of disturbance intensity or pre-disturbance plant community. The transition from herb to shrub dominance, which happened at about 14 years for Watershed 1 and never happened in Watershed 3, was determined primarily by the performance of the colonizing shrub *Ceanothus spp*. Of particular note is that the pre-disturbance plant community with a strong herb component never developed a shrub-dominant phase during early seral.

The most recent study in the HJA series examined understory vegetation dynamics through canopy closure, where Halpern and Lutz (2013) describe the plant communities in the HJA watersheds at ages 15 to 45 years. This study provides a glimpse at the response of well-studied plant communities through the stage of overstory canopy closure. The more traditional models of forest stand development (see earlier discussion) describe canopy closure as a critical point when the overstory tree canopy exerts strong controls on the understory plant community that result in the rapid decline in abundance and richness of understory species (Bormann and Likens 1979, Oliver and Larson 1996). However, contrary to that model, Halpern and Lutz (2013) found that while overstory cover increased 4-fold at the same time that understory plant abundance and richness declined 30-40%, the two were weakly linked. The understory decline was explained as much by the characteristics of the plant community as it was by overstory structure effects. The peak in richness and cover of all understory species was approximately 15 to 20 years after slash burning; at the same time the tree canopy cover was approximately 25-50%. After the peak, understory richness, cover, and biomass declined at approximately 10% per decade and was similar to pre-disturbance levels by the time the canopy closed. Halpern defined canopy closure as the peak in overstory tree cover, which for this study area was approximately 32 years for south aspects and 25 years for north aspects. The understory decline was led by early seral, shade intolerant, colonist species. Residual forest herbs changed little, and residual forest shrubs increased. Some of these trends mask changes in relative abundance among species within those groups.

Figure 8. The forest herb *Rubus ursinus* (trailing blackberry, family *Rosaceae*) as dense ground cover at the Watson Falls DEMO study site. See the boot for scale.

For example, the forest generalist herb (classified because it is a short shrub) *Rubus ursinus* (Figure 8) expanded rapidly following the initial disturbance.

An important result for this most recent study in the HJA was the high degree of plot-level variation in understory richness, cover, and biomass, which varied up to 2 orders of magnitude among the 188 plots. This variation suggests that comparing studies that are minimally replicated could potentially have show widely different results.

At the Starrbright site in the western Cascades of Oregon, Compagnoni and Halpern (2009) conducted a manipulative study to examine the relationships between exotic and native species in early seral. In their 24 control plots, they found that 16 years following clearcut and slash burning, total understory plant cover was approximately 15% in the first year, increased to greater than 70% in the second year and then slowly increased to approximately to 130% (sum of species' covers). Initial increases were led by herbs and subsequent slower but continual increase in cover was attributed to shrubs. In the main part of the study, they experimentally removed dominant native shrubs in the presence of important exotic species: *Crepis capillaris, Cirsium vulgare, Lactuca serriola*, and *Senecio sylvaticus*. They concluded that the successional dynamics of the native and exotic species in their study were not related. The exotic species were considered "weak" invaders that played a transient role in post-disturbance vegetation dynamics. Successful germination of exotics was determined by similar environmental factors as germination of native early seral plants. Exotics peaked at approximately 20% cover 6 years following disturbance.

West and Chilcote (1968) reported results from 10 years of monitoring understory vegetation following clearcut and slash burning at 24 sites near Mary's Peak in the Oregon Coast Range. They found a dramatic increase in total species canopy cover during the first 2 years that was dominated by *Senecio sylvaticus*. Total species canopy cover continued to increase at a slower pace for the remainder of the 10 year study period, while *Senecio sylvaticus* declined dramatically by the 3rd year.

The intensive forest management study (IFM) is a replicated manipulative experiment in plantation forests of the Oregon Coast Range (Betts et al. 2013, Stokely 2018). This study is collecting annual measurements of understory plant cover across a gradient of herbicide intensities. Results from the no-herbicide clearcut stands are included in this review as a comparison (Figure 12) with previously described clearcut studies from the Cascades.

Figure 9. The DEMO treatments at the Watson Falls site, western slope of the Oregon Cascades. Aggregates are 1 hectare circles. (*Google Earth photo August 2012*)

Retention harvest

The pre-treatment DEMO stands were mostly composed of Douglas-fir trees aged 65 to 170 years. Treatments included different levels and patterns of retention as shown in Figure 9 and described earlier. There was no broadcast burning following harvest, but some slash was removed at the sites with high slash loading. Herbicides were not used, and hand-planting was conducted with target densities ranging from 476 to 741 TPH (Aubry et al. 1999). Halpern et al. (2005) and Halpern et al. (2012) describe the initial responses (1-2 years post harvest) and longer term responses (6-11 years post harvest), respectively, of understory plants and bryophytes.

Halpern et al. (2005) reported large post-harvest changes in understory plant community structure (decreased total cover, shrub heights, and density of natural regeneration). The composition of the short-term post-harvest plant community was strongly influenced by pre-harvest conditions. However, there were still instances of local extirpations of late seral species. Late seral extirpations also occurred in the aggregates. There was little evidence for early responding early seral herbs and ruderal species in general. This result is an important difference between the response following clearcut and the response following VRH. The authors suggest this difference is due to the lack of broadcast burning and higher slash loading at the DEMO sites. Slash loading was up 80% cover at some sites.

General responses to treatment was that the magnitude of change of the understory plant community was greater with less retention (i.e. more similar to a traditional clearcut). The amount of retention was more important than the pattern of retention in describing plant responses. These general responses are described at the stand scale, meaning that the responses for the aggregated treatments are the mean response of both the cut and uncut portions of the aggregated treatment stands. Not surprisingly, the differences between the cut and uncut portions of the aggregated treatment stands were “large and statistically significant”. Plot to plot variation also increased at lower level of retention.

Longer-term responses for all DEMO treatments agreed with the earlier responses regarding the relative influence of pattern and amount of retention (Halpern et al. 2012). Figure 10 shows the responses of plant functional groups at approximately years 7 and 11. At the patch (sub-stand) scale, changes in the cut areas adjacent to the uncut aggregates were significantly greater than the changes in the dispersed treatments of the same retention level. Late seral herbs were sensitive to treatments and experienced local extirpations, while early seral species increased in abundance. Revegetation was rapid and many groups recovered in terms of cover and height within 6-10 years. Understory succession was dominated by colonizing early seral species along with the recovery of disturbance-tolerant forest herbs. Shrubs were slower to recover. Bryophyte cover decreased 20-60% regardless of treatment. This result agreed with the conclusion of a global meta-analysis of the effects of retention harvest on multiple taxa including bryophytes (Rosenvald and Lohmus 2008). Halpern et al. (2012) also reported general responses by classifying species into functional groups, as described earlier in this synthesis. Table 5 describes these responses along with a comparison to the functional group classification used in the H.J. Andrews studies described earlier. While the authors concluded that the 15% retention minimum standard for federal lands was too low to maintain late seral diversity, the corollary is that lower retention may increase early seral conditions.

In addition to describing general responses, the authors analyzed compositional changes within treatments using non metric multidimensional scaling. This is an ordination approach that examined relative degrees of change in the plant communities to the different treatments over time. Consistent with other analyses, the community change was greater at lower retention. Community change was also greater in the cut areas of aggregated treatments than in the dispersed stands for the same stand-level

seral stage	growth forms	corresponding HJA groups	group name	response, 6-11 years			
				15% dispersed	15% aggregated -cut	40% dispersed	40% aggregated -cut
early	herbs (including ferns and low-growing woody species)	I1, I2, I3, I4	*early seral herbs*	++	++		++
	tall shrubs	I4, I5, I6	*early seral shrubs*	+	+		+
forest	herbs (including ferns and low-growing woody species)	I4, R1, R2, R3, R4	*forest generalist herbs*	++	+	+	+
	tall shrubs	R3, R4	*forest generalist shrubs*	-	--		
late	herbs (including ferns and low-growing woody species)	R4, R5	*late seral herbs*	--	--		--
	bryophytes (mosses, liverworts)		*bryophytes*	--	--	--	--

Table 5 Response (canopy cover) of functional plant groups to some of the DEMO treatments. The plus symbols represent positive responses and the minus symbols represent negative responses. The number of symbols represent the relative size of the effect. “Cut” refers to the harvested sections of that aggregated treatment level. We included a comparison with the functional groups used in the HJA study (Halpern 1989) and also shown in Figures 6 and 7. Table modified from Figure 6 in Halpern et al. (2012).

retention amount. This important result suggests that community change will be greater following a clearcut than dispersed retention as low as 15%.

DEMO also provided an opportunity to study edge affects on vegetation dynamics. Murcia (1995) provides a general review of the ecological and conservation implications of forest edges. Nelson and Halpern (2005) measured the short-term (1-2 year) plant responses in the cut and uncut portions of the 40% aggregated treatments (Figure 11). Compared to pre-harvest, the cut areas lost 2 species and gained 9 early seral species, compared to a gain of 1 in the uncut patch. Recruitment of early seral species in the uncut patches were only observed within 10m of the edge. Early seral species richness approximately doubled between years one and two in both cut and uncut areas. Some orchids and ericaceous shrubs declined significantly in cleared areas. Because many of these are mycotrophs, the authors suggested that logged areas may have significant declines in mycorrhizal fungi. DEMO did not test different sized uncut patches, but based on a meta-analysis of retention harvest in temperate forests on 3 continents, Baker et al. (2016) found that changes in plant community composition in cleared areas adjacent to both uncut aggregates and large intact forest were similar, suggesting that the changes in adjacent plant communities do not depend upon aggregate size.

Heithecker and Halpern (2007), in a subset of the DEMO stands, noted that edge-induced changes in microclimate can extend as far as 40m into the 1 hectare uncut patches. In the HJA and the Wind River Experimental Forest in Washington, Chen et al. (1995) found that changes in solar radiation and soil moisture, 10-15 years post clearcut, could extend 30 to 60m into old growth patches and changes in relative humidity could extend up to 240m (the limit of their measurements). Chen et al. (1992) reported 240m as the maximum extent for edge-related microclimate influence and that their results agreed with other studies in the PNW. However, their results also show large variation in the range of “effective edge effect” (defined as a return to 2/3 of the original values). Effective edge effects ranged from 16 to 137m. Edge effects included increased mortality of residual trees, increased density of Douglas-fir and western hemlock, and rapid increase in overstory canopy cover. In DEMO, Maguire et al. (2006) noted increased exposure to unravelling (windthrow of trees on the edge of patches) for the 15% aggregated treatments.

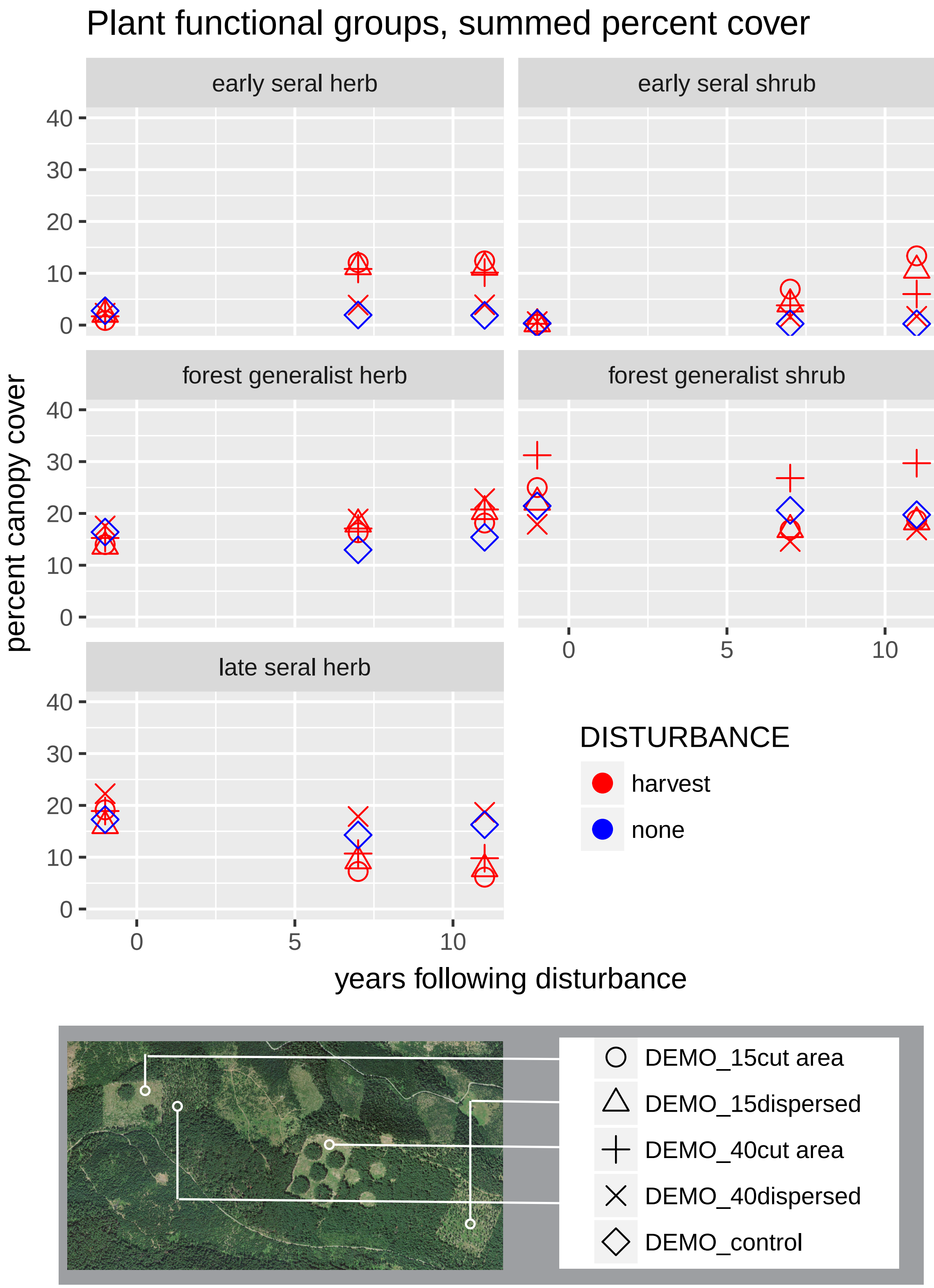


Figure 10. The response of plant functional groups to experimental retention levels and patterns in the DEMO study in the western Cascades. Cover represents the summed species cover by group in subplots, then averaged over plots and then treatment. "Cut area" is the harvested portion of an aggregated treatment, as shown in the photo. Halpern et al. 2012 provides more detail and figures showing proportional treatment responses. Data provided by Charles Halpern.

Figure 11. A 1-hectare patch and associated edge in the aggregated retention treatment of the DEMO study. Watson Falls site.

Fire

Bailey and Poulton (1968) measured plant responses 17 to 29 years following the Tillamook fires. The first Tillamook fire of 1933 was characterized as a severe crown fire that burned 99,000 hectares. Subsequent fires in 1939 and 1945 were of mixed severity and pattern that burned part of the original burn and an additional 45,000 hectares. All burned areas were native forest. Regeneration of Douglas-fir was considered exceptionally slow and significant reforestation efforts by aerial seeding and hand-planting were undertaken. Bailey and Poulton (1968) observed that plant community responses fell into 6 subjectively-defined plant associations based on the dominant species and topography as shown in Table 6. Vegetation responses (canopy cover) from this study are also included in Figure 12. Similar to the other studies already described, the authors for this study reported high plot-level variation in plant responses. Some areas of the Tillamook burns apparently have never recovered an understory plant community (T. Spies personal communication).

In the Warner Creek Fire study mentioned previously, Brown et al. (2013) found that 14 years post-fire, species richness included 15 trees, 35 shrubs, and over 70 herbs. Canopy cover values by functional group are shown in Figure 12 for both the Pacific silver fir (higher elevation) and western hemlock forested zones. The most abundant shrub was *Ceanothus velutinus* at 12% and 15% cover in the Pacific silver fire and western hemlock zones, respectively. Abundant herbs in the Pacific silver fir zone included *Tiarella trifoliata* (3% cover), *Anaphalis*

association	topography	mean percent cover of the associated species 1st spp	2nd spp
Alnus rubra / Polystichutm munitum	North aspect, lower portion of slopes, below 360m elevation	97	64
Alnus rubra / Rubus parviflorus	North aspect, steep slopes, usually higher than 360m	76	75
Acer circinatum / Polystichum mununitum	all aspects, steep lower portion of slopes, 210 - 360m elevation	38	24
Rubus parviflorus / Trientalis latifolia	all aspects, steep upper slope positions, above 360m	88	19
Pteridium aquilinum / Lotus crassifolius	all aspects, gentle middle to upper slopes, above 360m	81	53
Vaccinium parvifolium / Gaultheria shallon	South aspect, convex slopes or ridgetops, 210-360m elevation	17	42

Table 6. Plant associations (post-hoc) identified by Bailey and Poulton in 42 stands, 17 to 29 years following the Tillamook fires of 1933 to 1945.

margaritacea (3%), *Fragaria vesca* (2%). Abundant herbs in the western hemlock zone included *Lactuca muralis* (7%), various mosses (6%), and *Polystichum munitum* (2%). At 14 years, shrubs still had higher canopy cover than trees, although trees were overtopping the shrubs.

Other fire studies at the edge of our study area include the Hoh fire in Olympic Mountains and the Charlton fire on the crest of the Oregon Cascades. Following the 1978 Hoh fire, Huff (1995) found that *Senecio sylvaticus* was the dominant herb 2 and 3 years post-fire. The Torrey-Charlton Research Natural Area, at 1,700m elevation, is dominated by *Tsuga mertensiana*. The understory is mostly *Vaccinium scoparium* with a minimal herbaceous layer (Acker et al. 2013). In 1996, a severe but patchy fire burned 3,700 hectares. Tree mortality in the burned areas was over 90%. Fifteen years following the fire, the authors observed that small shrubs were the only understory vegetation in the unburned plots and the burned plots had a mix of small shrubs, graminoids, and forbs. Species diversity among all 12 plots was low: 6 forbs, 6 graminoids, and 2 shrubs. *Epilobium angustifolium* comprised 82% of the forb cover. *Carex rossii* comprised 85% percent of the graminoid cover, and *Vaccinium scoparium* comprised 98% of the shrub cover. Data from the Charlton fire was not included in Figure 12 because it cluttered the graph and the maximum canopy cover by group for any year never exceed 8%.

Additional Considerations

Seed Banks and Plant Propagules

Ingersoll and Wilson (1990) examined plant propagules (seed and vegetative sprouts) in the HJA. In the lab, they simulated variable levels of disturbance of soil and litter samples collected in forest stands up to 500 years old. The vast majority of emergents (88%) were from vegetative sprouts as opposed to seed. At higher disturbance levels, the relative dominance of emergents decreased. Seedling emergence was not affected by the level of disturbance. These results suggest a confirmation of our general model of post-disturbance vegetation dynamics: that residual forest species persist through disturbance, and the relative dominance of early seral colonists increases with increasing level of disturbance. Even in these older forest forests, *Senecio sylvaticus* was the most abundant species that germinated from seed.

In soil samples in mature forest stands in southwest British Columbia, McGee and Feller (1993) found abundant and widespread propagules of the forest generalist herbs *Gaultheria shallon* and *Athyrium felix-femina*, and the early seral herb *Senecio sylvaticus.* In contrast, *Senecio sylvaticus* did not germinate in the lab from soils collected by Kellmann (1970) in 100 year-old southwest British Columbia forests. This suggests that even though *Senecio sylvaticus* appears to be widespread, it may be locally absent in some forest stands or under specific conditions. Kellman also observed that most species that germinated in the lab from seed in forest and litter samples were not present in the actual stands.

Ceanothus velutinus has also been described as an important early seral shrub. In addition to the longevity of viable seed for *Senecio sylvaticus*, *Ceanothus velutinus* seed can remain viable for several hundred years (Gratkowski 1962). They also require heat for cracking the hard seed coat and successfully germinating (Zavitkovski 1968).

Halpern et al. (1999) also used the greenhouse emergence method to determine the diversity and abundance of the seed bank in forest litter and soil in 40-60 year old forests of the Olympic Mountains. They found that the seed bank in these forests were ubiquitous in terms of diversity but densities had a high degree of variability. Seeds for early seral species were more abundant than for residual forest and late seral species.

Variation in Disturbance

Exposure of mineral soils upon harvest has been shown to favor natural regeneration of Douglas-fir (Williamson 1973, Tappeiner 1997) and early seral species generally benefit from soil disturbance (Halpern et al. 2012). Variation in disturbance includes: the level and pattern of live and dead trees remaining, mechanical damage to residual vegetation from harvest activities (or fire), soil disturbance from both harvest activities and burning, piled vegetation from slash management, and replanting activities. Although not applicable for federal forests (see Table 1), the use of herbicides has a significant impact on vegetation dynamics by suppressing vegetation that competes with conifer crop species. Disturbance also has temporal variability because tree mortality, snag fall, and snag fragmentation can continue for many years following the primary harvest or fire disturbance (Maguire et al. 2006, Brown et al. 2013).

For the DEMO study, the different harvest systems (helicopter, suspended cable, ground-based loaders) caused variation in the amount of mechanical disturbance to retained vegetation and soils. In the DEMO Watson Falls unit, all slash except for a layer 5 to 15cm deep was moved off site and burned. Halpern and McKenzie found that slash accumulation was much higher in aggregated than dispersed retention. Morris (1958) and Steen (1966) found that shrub cover was higher in areas that where logging slash was burned compared to unburned, following clearcut.

In the Oregon Coast Range, Huffman et al. (1993) found that *Gaultheria shallon* (a forest generalist herb) in thinned stands had higher survival rates on rotten logs and stumps and lower germination in disturbed mineral soils. Because *Gaultheria shallon* increases rhizome biomass under increased light conditions, it is a good example of a residual forest species that is released upon harvest or fire.

Environmental Variables

From one of the studies in the HJA, Halpern and Lutz (2013) noted some important differences between north and south aspect slopes. They found that understory biomass declined on the south but not on the north aspect slopes, and had higher initial biomass on south aspects. They also found that canopy closure occurred approximately 10 years earlier on the north aspect slopes, along with higher tree densities on the north aspects. One possible explanantion they suggested is the aspect-specific responses of *Ceanothus spp*. *Ceanothus* prefers warmer sites and is relatively shade intolerant. The seed bank of *Ceanothus* may have been more abundant on the south aspects, again reinforcing the pre-disturbance community control over subsequent succession. Aspect may also influence the prevalence of other species: shade-tolerant *Acer* on north and moister slopes and *Rhododendron* and *Corylus* on south and drier slopes.

Landscape context

There is a general paucity of research that examines the landscape context of biodiversity responses to retention harvest (Rosenvald and Lohmus 2008, Gustafsson et al. 2012, Mori et al. 2017). Mori et al. (2017) conducted a global meta-analysis of 31 cases studies that involved multiple taxa. They found that stand-scale retention level was the most important covariate in predicting the biodiversity responses to retention harvest. However, including a landscape variable of forest versus non-forest improved the predictive performance of their model.

Herbivory and pollination are additional landscape factors that have been poorly studied. The ongoing IFM study in the Oregon Coast Range has the potential to shed light on the influence of wide-ranging ungulate herbivores on plant community dynamics in harvested stands. Herbivory on conifers has already been mentioned as one of the three primary causes of mortality in regenerating conifers from both fire and harvest. Immediately following natural regeneration from clearcut harvest in the HJA, Gashwiler (1971) found that animal damage (mostly small mammals) was the number one cause of Douglas-fir seedling mortality.

Synthesis of Empirical Studies

Conclusions

Comparing studies and treatments

In order to aid our synthesis of the many studies reviewed in this document we combined the canopy cover measures of functional group responses in a master figure (Figure 12). Several caveats are important to consider when interpreting this figure: 1) the variation of plot-level responses for each study are not shown, 2) data for the pre-disturbance plant communities were only available for the HJA and DEMO studies, 3) sampling methodology varies by study, and 4) species assignments to functional groups may be interpreted differently by other researchers. After considering these caveats, some general trends are evident. The responses from the Cascades (HJA) and Coast Range studies (IFM) are similar, at least for the first five years of available data for the IFM study. This suggest that relative responses to harvest treatments may be similar during early seral. The responses from the DEMO VRH study, however, differ from the clearcut studies except for forest generalist shrubs. Possible explanations are provided below. The paucity of fire studies are evident in the figure. The herb responses at the Tillamook site are a bit of a mystery. Possible explanations include dominance by a few species or a sampling effect. The early seral herb response is composed of mostly *Hosackia crassifolius* (19%), *Elymus glaucus* (11%), and *Anaphalis margaritacea* (8%). The forest generalist herb response is composed of mostly *Polystichum munitum* (23%) and *Rubus ursinus* (22%).

Vegetation dynamics model

Conclusions from the empirical studies we reviewed support our conceptual model of the vegetation dynamics following disturbance in our region (Figure 2). The pre-disturbance plant community plays a significant role, particularly for forest residual species, in post-disturbance vegetation succession, rate, and trajectory. The response of colonizing early seral shrubs and herbs is more dependent upon the level of disturbance. For example, seeds of both *Senecio sylvaticus* (an early seral herb) and *Ceanothus velutinus* (an early seral shrub) are typically present for long times in forest soils and therefore have the potential to be abundant germinants given the right disturbance conditions. For herb-dominated pre-disturbance communities, the potential is for herb dominance through early seral. For shrub-dominated pre-disturbance communities, the potential is for delayed shrub dominance following an initial herb dominance stage. Tree-dominated pre-disturbance communities are more destined for rapid tree establishment and canopy closure. The level of disturbance modifies this “pre-ordained” early seral trajectory through three mechanisms: 1) mechanically damaging residual species, 2) modifying the environment so that sensitive residual species are extirpated or greatly reduced in abundance, and perhaps most importantly 3) creating conditions conducive to establishment of early seral colonists. Minimally-disturbed sites will develop in ways that reflect the forest residuals that survived. More heavily disturbed sites will not lose all forest residuals, but early seral colonists will dominate early succession. The pre-disturbance plant community and the level of disturbance should be considered the primary factors affecting early seral plant communities. Other factors that will play a role include the availability of seed from off-site sources, herbivory, species interactions, and stochastic climatic events.

Variability

Nearly all the studies we reviewed noted significant variability in either or both of the plot and stand level responses to disturbance. This should not be surprising as variability seems ubiquitous in many ecological studies. However, it strongly suggests that predicting the vegetation dynamics to the multiple management-induced and environmental factors in our conceptual model (Figure 2) must allow for a

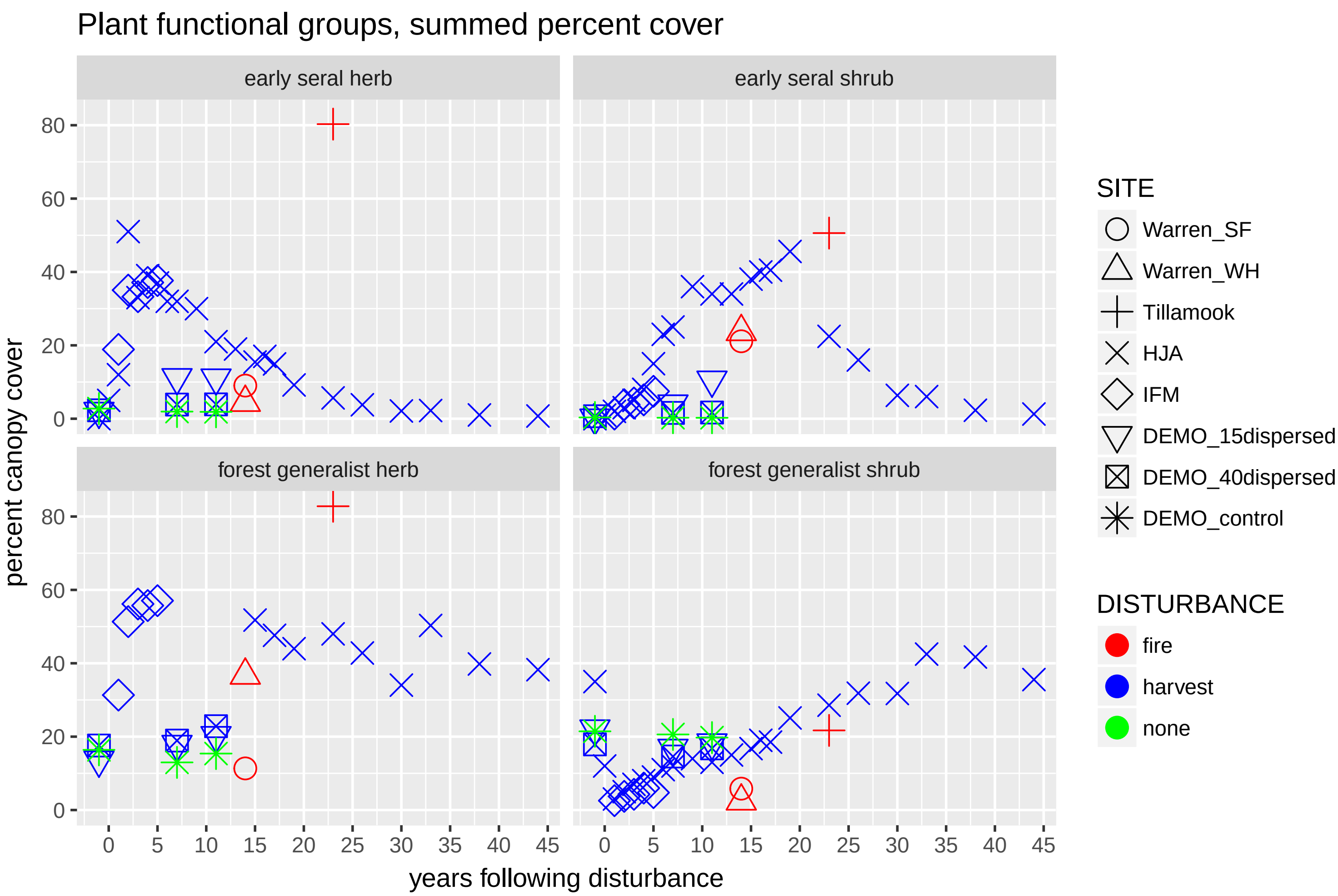


Figure 12. Comparison of plant functional group responses to several studies described in the text and in Table 2. Warner-SF is from the higher elevation Pacific silver fir forest zone and Warner-WH is from the western hemlock forest zone. The Tillamook fire data spans a range of 17 to 29 years but the average of 23 years is plotted on this figure. Functional groups were assigned based on the DEMO assignments and described in Halpern et al. (2012) and listed in the Appendix of this review. For species not present in DEMO, group assignments followed information provided by Stokely et al. (2018) or assigned by this author (SH). Canopy cover represents the additive species cover within each group. For some studies, the raw data available was canopy cover by group. Data sources include data provided by primary authors (IFM, DEMO), appendices to published studies (HJA 15 to 44 years), and data extracted from published tables (Tillamook) and figures (HJA -1 to 16 years) Specific methods for calculating means and sampling notes for each study are included in the Appendix. HJA data for forest generalist herbs were not available for years -1 to 15.

range of responses.

Establishment, canopy closure, and the duration of early seral

A typical establishment period for post-fire tree cohorts has been shown to last approximately 20 to 60 years. In the one study that described canopy closure, the authors noted that canopy closure took an additional 20 years. The protracted establishment model has not been refuted, but current studies suggest protracted- or non-establishment is an exception.

Following clearcut harvest, two studies showed that canopy closure occurred between approximately 20 and 40 years. This suggests that compared to natural fire disturbance, establishment and canopy closure occurs more rapidly following harvest. One study concluded that canopy closure occurred approximately 20 years sooner in the Oregon Coast Range than the Cascades. This difference may be due to the higher productivity of forests in the Oregon Coast Range (Spies et al. 2002). However, a comparison of the responses in the IFM study with the HJA study suggest that the understory plant responses are very similar early in succession.

As previously mentioned, canopy closure should not be considered as a discrete point in time when early seral values terminate. Canopy closure affects the understory plant community, but additional factors including plant community interactions may be equally or more important.

Fire versus Clearcut versus VRH

Due to the paucity of post-fire studies, it is challenging to compare post-fire to post-VRH and post-clearcut responses. However, the differences between the post-clearcut and post-VRH responses are most likely due to the differences in disturbance between these two treatments. Fire severity has been shown to have an important influence on vegetation dynamics. Slash at all the clearcut study sites was burned whereas at DEMO it was not. Other factors that could explain the different responses of DEMO from clearcut are that DEMO has more retained live and dead trees and higher slash and coarse woody debris loading. If our hypothesis of the role of fire is true, then ***VRH treatments should consider implementing fire in order to more closely emulate natural disturbance***.

Research Recommendations

Our review and synthesis of the research literature suggest several avenues for future research:

- There is a paucity of post-fire studies that measure annual plant responses. The Charlton fire is an exception because that study provided annual data for the first 15 years following fire. However, the Charlton study is at a high elevation site and vegetation dynamics are likely different from the majority of our study area. Fine temporal scale post-fire data would allow for effective comparisons between VRH and fire disturbance.
- The absence of pre-fire plant community data would limit the ability to infer vegetation dynamics from post-fire studies. Therefore, any opportunities for retrospective studies would be invaluable.
- The IFM study in the Coast Range should be continued through canopy closure. Other studies have shown that canopy closure occurs more rapidly in the Coast Range. Therefore, it would be valuable to compare the closure dynamics in the Coast Range with the already-studied closure dynamics in the Cascades. This would also capitalize on the well-replicated design of the IFM study.
- Studies should be implemented in VRH stands that manipulate levels of fire disturbance and slash loading. These type of studies would test the hypothesis that the difference between the post-clearcut and post-VRH responses is due to those factors.
- Monitoring should be conducted in operational VRH stands in order to test whether any difference in responses are due to harvest prescriptions versus experimental designs. For example, operational prescriptions may involve a manager specifically choosing an aggregate site for a specific objective.
- Studies should be implemented that examine the role of retention structures (e.g. perches, nests) in seed dispersal and associated vegetation dynamics.
- The potential for the surrounding landscape to mediate stand-level responses should be examined.
- The early seral values that are most important to manage for and conserve should be explicity described. Currently, the assumption is that the early seral values can be maximized if VRH can emulate natural fire disturbance. However, early seral values may vary spatially and temporally in ways that are not sufficiently described by disturbance.

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Citations

See the annotated bibliography .xls file

Appendices

The following pages include the complete plant list for the studies synthesized in Figure 12. Functional group assignments for 312 species follow the assignments for the DEMO study (Halpern et al. 2012) and were provided by Charles Halpern. Additional assignments for species not present at the DEMO sites were made from information provided by Thomas Stokely or subjectively assigned by the primary author, Scott Harris. Herb groups include graminoids, ferns, and short shrubs.

Notes describing the methods used to summarize data for Figure 12 are also included.

Group	Species	Common name	Family
tree	Abies amabilis	Pacific silver fir	Pinaceae
tree	Abies concolor	White fir	Pinaceae
tree	Abies grandis	Grand fir	Pinaceae
tree	Abies lasiocarpa	Subalpine fir	Pinaceae
tree	Abies magnifica	Red fir	Pinaceae
tree	Abies procera	Noble fir	Pinaceae
forest generalist shrub	Acer circinatum	Vine maple	Aceraceae
forest generalist shrub	Acer glabrum	maple	Aceraceae
tree	Acer macrophyllum	Bigleaf maple	Aceraceae
unclassified herb	Achillea millefolium		
late seral herb	Achlys triphylla	Vanilla leaf	Berberidaceae
forest generalist herb	Actaea elata	Tall bugbane	Ranunculaceae
forest generalist herb	Actaea rubra	Red baneberry	Ranunculaceae
late seral herb	Adenocaulon bicolor	Trailplant, pathfinder	Asteraceae
forest generalist herb	Adiantum pedatum		
unclassified herb	Agoseris elata		Asteraceae
unclassified herb	Agoseris grandiflora	Bigflower agoseris	Asteraceae
early seral herb	Agoseris heterophylla		Asteraceae
early seral herb	Agrostis alba		Poaceae
early seral herb	Agrostis exarata	Spike bentgrass	Poaceae
early seral herb	Agrostis scabra		Poaceae
early seral herb	Agrostis spp		Poaceae
early seral herb	Agrostis tenuis		Poaceae
early seral herb	Aira caryophyllea	Silver hairgrass	Poaceae
late seral herb	Allotropa virgata		
tree	Alnus rubra	Red alder	Betulaceae
unclassified shrub	Alnus sinuata		
unclassified shrub	Amelanchier alnifolia	Saskatoon serviceberry	Rosaceae
early seral herb	Anaphalis margaritacea	Pearly everlasting	Asteraceae
forest generalist herb	Anemone deltoidea	Columbian windflower	Ranunculaceae
forest generalist herb	Anemone lyallii		
early seral herb	Antennaria racemosa		
unclassified herb	Apocynum androsaemifolium		
unclassified herb	Aquilegia formosa	Western columbine	Ranunculaceae
early seral herb	Arabis glabra		
early seral herb	Aralia californica		
early seral shrub	Arctostaphylos columbiana		
unclassified herb	Arctostaphylos nevadensis		
early seral shrub	Arctostaphylos patula		
unclassified herb	Arctostaphylos uva-ursi		
forest generalist herb	Arenaria macrophylla		
forest generalist herb	Arnica latifolia		
early seral herb	Arunclassifiedus sylvester		
late seral herb	Asarum caudatum	Wild ginger	Aristolochiaceae
late seral herb	Asarum hartwegii		
unclassified herb	Aspidotis densa		

Group	Species	Common name	Family
unclassified herb	Aster occidentalis		
unclassified herb	Aster radulinus		
forest generalist herb	Athyrium filix-femina	Common ladyfern	Dryopteridaceae
forest generalist shrub	Berberis aquifolium	Oregon grape	Berberidaceae
forest generalist herb	Berberis nervosa	Dwarf Oregon grape	Berberidaceae
late seral herb	Blechnum spicant	Deerfern	Blechnaceae
late seral herb	Boschniakia strobilacea		
early seral herb	Boykinia elata		
early seral herb	Brachypodium sylvaticum		
early seral herb	Brodiaea congesta		
unclassified herb	Bromus carinatus		
forest generalist herb	Bromus vulgaris	Columbia brome	Poaceae
tree	Calocedrus decurrens		
forest generalist herb	Calypso bulbosa		
forest generalist herb	Campanula scouleri	Scouler's hairbells, bellflower	Campanulaceae
forest generalist herb	Cardamine angulata		
early seral herb	Cardamine oligosperma		
unclassified herb	Carex brunnescens		Cyperaceae
forest generalist herb	Carex concinnoides		Cyperaceae
forest generalist herb	Carex deweyana		Cyperaceae
unclassified herb	Carex disperma		Cyperaceae
unclassified herb	Carex fracta		Cyperaceae
unclassified herb	Carex hendersonii	Henderson's sedge	Cyperaceae
forest generalist herb	Carex laeviculmis		Cyperaceae
unclassified herb	Carex limnophila		Cyperaceae
unclassified herb	Carex mertensii		Cyperaceae
unclassified herb	Carex microptera		Cyperaceae
unclassified herb	Carex pachystachya	Thick-headed sedge	Cyperaceae
unclassified herb	Carex pensylvanica		Cyperaceae
early seral herb	Carex rossii	Ross' sedge	Cyperaceae
early seral herb	Carex spp	Carex	Cyperaceae
early seral herb	Carex spp	Carex	Cyperaceae
early seral herb	Carex spp	Carex	Cyperaceae
tree	Castanopsis chrysophylla		
unclassified herb	Castilleja applegatei		
early seral shrub	Ceanothus cordulatus		Rhamnaceae
early seral shrub	Ceanothus integerrimus		Rhamnaceae
early seral shrub	Ceanothus sanguineus		Rhamnaceae
early seral shrub	Ceanothus velutinus	Snowbrush ceanothus	Rhamnaceae
early seral herb	Cerastium arvense		
early seral herb	Cerastium glomeratum	Sticky chickweed	Caryophyllaceae
early seral herb	Cerastium spp		
early seral herb	Cerastium viscosum		
early seral herb	Cerastium vulgatum		
early seral herb	Cerastium vulgatum		
tree	Chamaecyparis nootkatensis		

Group	Species	Common name	Family
late seral herb	Chimaphila menziesii		
late seral herb	Chimaphila umbellata		
early seral herb	Chrysanthemum leucanthemum		
unclassified herb	Cinna latifolia	Drooping woodreed	Poaceae
forest generalist herb	Circaea alpina		
early seral herb	Cirsium arvense	Canadian thistle	Asteraceae
unclassified herb	Cirsium callilepis		Asteraceae
early seral herb	Cirsium vulgare	Bull thistle	Asteraceae
late seral herb	Claytonia sibirica	Siberian springbeauty	Portulacaceae
early seral herb	Clinopodium douglasii	Yerba buena	Lamiaceae
early seral herb	Clinopodium douglasii	Yerba buena	Lamiaceae
late seral herb	Clintonia uniflora		
unclassified herb	Collinsia grandiflora		
unclassified herb	Collinsia parviflora		
unclassified herb	Collomia grandiflora		Polemoniaceae
early seral herb	Collomia heterophylla	Variableleaf collomia	Polemoniaceae
unclassified herb	Collomia linearis		Polemoniaceae
early seral herb	Convolvulus nyctagineus		
unclassified	Coptis laciniata	Oregon goldthread	Ranunculaceae
late seral herb	Corallorhiza maculata		
late seral herb	Corallorhiza mertensiana		
late seral herb	Corallorhiza striata		
late seral herb	Cornus canadensis	Bunchberry dogwood	Cornaceae
tree	Cornus nuttallii	Pacific dogwood	Cornaceae
forest generalist shrub	Corylus cornuta	Beaked hazelnut	Betulaceae
late seral herb	Crepis capillaris	Smooth hawksbeard	Asteraceae
early seral herb	Cryptantha affinis		
early seral herb	Cynosurus echinatus	Biristly dogtail grass	Poaceae
forest generalist herb	Cystopteris fragilis		
early seral herb	Dactylis glomerata	Orchardgrass	Poaceae
unclassified herb	Daucus carota	Queen Anne's lace	Apiaceae
unclassified herb	Delphinium nuttallianum		
forest generalist herb	Deschampsia cespitosa	Tufted hairgrass	Poaceae
forest generalist herb	Deschampsia danthonioides	Annual hairgrass	Poaceae
early seral herb	Deschampsia elongata		
forest generalist herb	Dicentra formosa	Bleeding heart	Fumariaceae
early seral herb	Digitalis purpurea	Foxglove	Scrophulariaceae
late seral herb	Disporum hookeri		
late seral herb	Eburophyton austiniae		
early seral herb	Elymus glaucus	blue wildrye	Poaceae
early seral herb	Epilobium angustifolium	Fireweed	Onagraceae
early seral herb	Epilobium brachycarpum	Tall annual willowherb	Onagraceae
early seral herb	Epilobium ciliatum	Fringed willowherb	Onagraceae
early seral herb	Epilobium minutum		Onagraceae
early seral herb	Epilobium paniculatum		Onagraceae
early seral herb	Epilobium watsonii		Onagraceae

Group	Species	Common name	Family
early seral herb	Equisetum palustre		
early seral herb	Equisetum spp		
unclassified herb	Equisetum telmateia		
early seral herb	Erechtites minima	Coastal burnweed	Asteraceae
unclassified	Erigeron canadensis		
unclassified herb	Eriophyllum lanatum		
unclassified herb	Erythronium oregonum	White fawnlily	Liliaceae
early seral herb	Festuca bromoides		
unclassified herb	Festuca idahoensis		
early seral herb	Festuca myuros		
forest generalist herb	Festuca occidentalis		
unclassified herb	Festuca rubra		
unclassified herb	Festuca subulata		
forest generalist herb	Festuca subuliflora		
early seral herb	Fragaria spp		
early seral herb	Fragaria vesca	Woodland strawberry	Rosaceae
tree	Fraxinus latifolia	Oregon ash	Oleacea
forest generalist herb	Galium aparine	Cleavers, sticky willy	Rubiaceae
forest generalist herb	Galium oreganum	Oregon bedstraw	Rubiaceae
forest generalist herb	Galium triflorum	Sweet-scented bedstraw	Rubiaceae
forest generalist herb	Gaultheria ovatifolia		
forest generalist herb	Gaultheria shallon	Salal	Ericaceae
early seral herb	Gayophytum diffusum		
unclassified herb	Geranium carolinianum	Carolina geranium	Geraniaceae
unclassified herb	Geum macrophyllum		
unclassified herb	Gilia capitata		
early seral herb	Gnaphalium microcephalum		
early seral herb	Gnaphalium purpureum		
late seral herb	Goodyera oblongifolia		
forest generalist herb	Gymnocarpium dryopteris		
unclassified herb	Habenaria saccata		
forest generalist herb	Habenaria unalascensis		
late seral herb	Hemitomes congestum		
unclassified herb	Heuchera micrantha		
forest generalist herb	Hieracium albiflorum	White hawkweed	Asteraceae
unclassified herb	Hieracium scouleri		
forest generalist herb	Holcus lanatus	Velvetgrass	Poaceae
early seral herb	Holcus spp		
forest generalist shrub	Holodiscus discolor	Oceanspray	Rosaceae
unclassified herb	Horkelia fusca		
forest generalist herb	Hydrophyllum tenuipes		
unclassified herb	Hypericum formosum		
early seral herb	Hypericum perforatum	St. Johnswort	Clusiaceae
early seral herb	Hypochaeris radicata	Hairy cat's ear	Asteraceae
late seral herb	Hypopitys monotropa		
forest generalist herb	Iris chrysophylla		

Group	Species	Common name	Family
forest generalist herb	Iris tenax	Toughleaf iris	Iridaceae
early seral herb	Junclassifiedus effusus		
unclassified herb	Junclassifiedus ensifolius		
unclassified herb	Junclassifiedus spp		
unclassified herb	Kelloggia galioides		
forest generalist herb	Lactuca muralis		
early seral herb	Lactuca serriola	Prickly lettuce	Asteraceae
early seral herb	Lathyrus nevadensis	Sierra pea	Fabaceae
unclassified herb	Lathyrus nevadensis		
early seral herb	Lathyrus polyphyllus		
early seral herb	Leucanthemum vulgare	Oxeye daisy	Asteraceae
forest generalist herb	Liliaceae spp		
unclassified herb	Lilium columbianum	Tiger lily/ Columbia lily	Liliaceae
unclassified herb	Lilium washingtonianum		
forest generalist herb	Linnaea borealis	Twinflower	Caprifoliaceae
late seral herb	Listera caurina		
late seral herb	Listera cordata		
early seral herb	Lolium multiflorum		
unclassified herb	Lonicera ciliosa	Orange honeysuckle	Caprifoliaceae
early seral herb	Lotus corniculatus		
early seral herb	Lotus crassifolius	Big deervetch	Fabaceae
early seral herb	Lotus micranthus	Desert deervetch	Fabaceae
early seral herb	Lotus purshiana		
forest generalist herb	Lupinus arcticus	Broadleaf lupine	Fabaceae
unclassified herb	Lupinus latifolius		
unclassified herb	Lupinus lepidus		
early seral herb	Luzula campestris		
unclassified herb	Luzula comosa	Pacific woodrush	Juncaceae
unclassified herb	Luzula divaricata		
late seral herb	Luzula multiflora	Common woodrush	Juncaceae
forest generalist herb	Luzula parviflora	Smallflowered woodrush	Juncaceae
forest generalist herb	Lycopodium clavatum		
forest generalist herb	Lysichitum americanum		
early seral herb	Madia gracilis	Grassy tarweed	Asteraceae
forest generalist herb	Mahonia nervosa	Dull Oregon grape	Berberidaceae
forest generalist herb	Maianthemum bifolium		
forest generalist herb	Maianthemum dilatatum	False lily of the valley	Liliaceae
forest generalist herb	Maianthemum stellatum	Starry false lily of the valley	Liliaceae
unclassified herb	Medicago lupulina	Black medick	Lamiaceae
forest generalist herb	Melica aristata		
early seral herb	Melica harfordii	Harford's oniongrass	Poaceae
forest generalist herb	Melica smithii		
forest generalist herb	Melica subulata		
forest generalist shrub	Menziesia ferruginea		
unclassified herb	Mertensia ciliata		
unclassified herb	Microsteris gracilis		

Group	Species	Common name	Family
unclassified herb	Mimulus guttatus		
unclassified herb	Mimulus moschatus	Muskflower	Scrophulariaceae
forest generalist herb	Mitella breweri		
forest generalist herb	Mitella diversifolia		
forest generalist herb	Mitella ovalis		
forest generalist herb	Mitella pentandra		
forest generalist herb	Mitella trifida		
late seral herb	Monotropa uniflora		
unclassified herb	Montia cordifolia		
unclassified herb	Montia parvifolia		
early seral herb	Montia perfoliata		
early seral herb	Montia sibirica		
early seral herb	Mycelis muralis	Wall lettuce	Asteraceae
early seral herb	Nemophila parviflora	Smallflower nemophila	Hydrophyllaceae
forest generalist herb	Nothochelone nemorosa		
unclassified shrub	Oemleria cerasiformis	Indian plum	Rosaceae
forest generalist shrub	Oplopanax horridum		
early seral herb	Osmorhiza berteroi	Sweet cicily	Apiaceae
forest generalist herb	Osmorhiza chilensis		
forest generalist herb	Osmorhiza purpurea		
forest generalist herb	Oxalis oregana	Redwood sorrel	Oxalidaceae
forest generalist herb	Pachistima myrsinites		
forest generalist herb	Pedicularis racemosa		
unclassified herb	Penstemon attenuatus		
unclassified herb	Penstemon deustus		
unclassified herb	Penstemon procerus		
unclassified herb	Perideridia parishii	Parish's yampah	Apiaceae
early seral herb	Petasites frigidus		
early seral herb	Phacelia heterophylla		
unclassified herb	Phacelia nemoralis	Shade phacelia	Hydrophyllaceae
early seral herb	Phacelia spp		
early seral herb	Phleum pratense		
early seral herb	Phlox adsurgens		
unclassified shrub	Physocarpus capitatus		
tree	Picea engelmannii		
tree	Pinus contorta	Lodgepole pine	Pinaceae
tree	Pinus monticola		Pinaceae
tree	Pinus ponderosa	Ponderosa pine	Pinaceae
early seral herb	Plantago lanceolata		
late seral herb	Pleuricospora fimbriolata		
early seral herb	Poa compressa	Canada bluegrass	Poaceae
unclassified herb	Poa palustris		
early seral herb	Poa pratensis	Kentucky bluegrass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae

Group	Species	Common name	Family
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae	Grass	Poaceae
unclassified herb	Poaceae spp		
early seral herb	Polygonum douglasii		
early seral herb	Polygonum minimum		
early seral herb	Polygonum nuttallii		
forest generalist herb	Polystichum munitum	Swordfern	Dryopteridaceae
tree	Populus trichocarpa		
unclassified herb	Potentilla glandulosa		
unclassified herb	Potentilla gracilis		
late seral herb	Prosartes hookeri	Hooker's fairybells	Liliaceae
early seral herb	Prunella vulgaris	Common selfheal	Lamiaceae
tree	Prunus emarginata	Bitter cherry	Rosaceae
tree	Prunus virginiana		
tree	Pseudotsuga menziesii	Douglas-fir	Pinaceae
tree	Pseudotsuga menziesii	Douglas-fir	Pinaceae
tree	Pseudotsuga menziesii	Douglas-fir	Pinaceae
early seral herb	Pteridium aquilinum	Western brackenfern	Dennstaedtiaceae
late seral herb	Pterospora andromedea		
unclassified herb	Puccinellia pauciflora		
late seral herb	Pyrola aphylla		
late seral herb	Pyrola asarifolia		
late seral herb	Pyrola chlorantha		
late seral herb	Pyrola picta		
late seral herb	Pyrola secunda		
late seral herb	Pyrola uniflora		
early seral herb	Ranunclassifiedulus unclassifiedinatus		
tree	Rhamnus purshiana	Cascara buckthorn	Rhamnaceae
forest generalist shrub	Rhododendron macrophyllum	Pacific Rhododendron	Ericaceae
early seral shrub	Rhus diversiloba		

Group	Species	Common name	Family
early seral shrub	Ribes binominatum		Grossulariaceae
early seral shrub	Ribes cereum		Grossulariaceae
early seral shrub	Ribes cruentum		Grossulariaceae
early seral shrub	Ribes lacustre	Prickly currant	Grossulariaceae
early seral shrub	Ribes lobbii	Gummy gooseberry	Grossulariaceae
early seral shrub	Ribes sanguineum	Redflower currant	Grossulariaceae
early seral shrub	Ribes viscosissimum		Grossulariaceae
unclassified shrub	Ribes watsonianum		Grossulariaceae
forest generalist shrub	Rosa gymnocarpa	Dwarf rose	Rosaceae
unclassified shrub	Rosa nutkana		Rosaceae
early seral shrub	Rubus armeniacus	Himalayan blackberry	Rosaceae
early seral shrub	Rubus laciniatus	Cutleaf blackberry	Rosaceae
late seral herb	Rubus lasiococcus		Rosaceae
early seral shrub	Rubus leucodermis	Whitebark rasberry	Rosaceae
late seral herb	Rubus nivalis	Snow rasberry	Rosaceae
early seral shrub	Rubus parviflorus	Thimbleberry	Rosaceae
forest generalist herb	Rubus pedatus		Rosaceae
early seral shrub	Rubus spectabilis	Salmonberry	Rosaceae
forest generalist herb	Rubus ursinus	Trailing blackberry	Rosaceae
early seral herb	Rumex acetosella	Sheep sorrel	Polygonaceae
early seral shrub	Salix scouleriana		Salicaceae
early seral shrub	Salix sitchensis	Sitka willow	Salicaceae
early seral shrub	Salix sp.	Willow	Salicaceae
early seral shrub	Sambucus caerulea	Blue elderberry	Caprifoliaceae
early seral shrub	Sambucus cerulea		
early seral shrub	Sambucus racemosa	Red elderberry	Caprifoliaceae
forest generalist herb	Satureja douglasii		
unclassified herb	Saxifraga punclassifiedtata		
unclassified herb	Scirpus microcarpus		
unclassified herb	Sedum oreganum		
forest generalist herb	Senecio bolanderi		
early seral herb	Senecio jacobaea	Tansy ragwort	Asteraceae
early seral herb	Senecio sylvaticus	Wood groundsel	Asteraceae
unclassified herb	Senecio triangularis		
late seral herb	Smilacina racemosa		
late seral herb	Smilacina stellata		
early seral herb	Sonchus asper	Spiny sow thisle	Asteraceae
forest generalist shrub	Sorbus scopulina		
forest generalist shrub	Sorbus sitchensis		
unclassified shrub	Spiraea betulifolia		
unclassified shrub	Spiraea douglasii		
unclassified herb	Stachys cooleyae	Coastal hedgenettle	Lamiaceae
unclassified herb	Stachys mexicana		
unclassified herb	Stellaria calycantha		
unclassified herb	Stellaria crispa		
unclassified herb	Stipa occidentalis		

Group	Species	Common name	Family
late seral herb	Streptopus amplexifolius	Claspleaf twistedstalk	Liliaceae
late seral herb	Streptopus roseus		
forest generalist herb	Symphoricarpos hesperius	Trailing snowberry	Caprifoliaceae
forest generalist herb	Symphoricarpos mollis		
late seral herb	Synthyris reniformis		
unclassified herb	Taraxacum ceratophorum		
early seral herb	Taraxacum officinale		
tree	Taxus brevifolia		
early seral herb	Tellima grandiflora	Bigflower tellima	Saxifragaceae
tree	Thuja plicata		
late seral herb	Tiarella trifoliata		
early seral herb	Torilis arvensis	Spreading hedgeparsley	Apiaceae
forest generalist herb	Toxicodendron diversilobum	Poison oak	Anacardiaceae
early seral herb	Tragopogon dubius		
forest generalist herb	Trautvetteria caroliniensis		
forest generalist herb	Trientalis borealis ssp. latifolia	Broadleaf starflower	Primulaceae
forest generalist herb	Trientalis latifolia		
early seral herb	Trifolium repens	White clover	Fabaceae
late seral herb	Trillium ovatum	Pacific trillium	Liliaceae
forest generalist herb	Trisetum canescens		
forest generalist herb	Trisetum cernuum		
tree	Tsuga heterophylla	Western hemlock	Pinaceae
tree	Tsuga mertensiana		
forest generalist shrub	Vaccinium membranaceum		Ericaceae
forest generalist shrub	Vaccinium ovalifolium	Oval leaf blueberry	Ericaceae
forest generalist shrub	Vaccinium parvifolium	Red huckleberry	Ericaceae
forest generalist herb	Vaccinium scoparium	Grouse whortleberry	Ericaceae
early seral herb	Valeriana scouleri		
unclassified herb	Valeriana sitchensis		
late seral herb	Vancouveria hexandra	Golden inside-out flower	Berberidaceae
early seral herb	Verbascum thapsus		
unclassified herb	Veronica americana		
unclassified herb	Veronica arvensis		
early seral herb	Veronica officinalis		
early seral herb	Veronica peregrina		
early seral herb	Veronica serpyllifolia	Thymeleaf speedwell	Scrophulariaceae
unclassified herb	Vicia americana	American vetch	Fabaceae
unclassified herb	Vicia cracca	Bird vetch	Scrophulariaceae
unclassified herb	Vicia hirsuta	Tiny vetch	Fabaceae
unclassified herb	Vicia sativa	Garden vetch	Fabaceae
forest generalist herb	Viola adunclassifieda		
forest generalist herb	Viola glabella		
forest generalist herb	Viola orbiculata		
forest generalist herb	Viola sempervirens	Evergreen violet	Violaceae
forest generalist herb	Viola spp		
unclassified herb	Vulpia bromoides	Brome fescue	Poaceae

Group	Species	Common name	Family
forest generalist herb	Whipplea modesta		
forest generalist herb	Woodsia oregana		
forest generalist herb	Xerophyllum tenax		

Data reduction notes for Figure 12

IFM data, 1- 5 years, Stokely et al. (in review)

1. Data provided by Thomas Stokely
2. Circular plots, ocular estimates of cover by species
3. Species cover in each plot: 5 years, 7 stands, 12 plots
4. Assign species to groups, just use the 4 groups (ESH, ESS, FGH, FGS)
5. For each plot, sum species cover in each group
6. Ensure that each year.stand.plot.group has a number (may need to merge to get zeros): 1680 rows
7. Get the stand mean from the 12 plots, for each group
8. Get the group mean: end up with 4 means for each of 5 years: 20 rows

Charlton, 1-15 years (Acker et al. 2017)

1. Data provided by Rob Pabst
2. 9 circular plots, 2 lines per plot, line-intercept method
3. Of 9 plots, 6 are burned (crown fire) and 3 are control
4. Species cover for each plot: 15 years, 9 plots
5. Assign species to groups, only need 2 groups (ESS, FGS) because no shrubs!
6. For each plot, sum species cover in each group
7. Ensure that each year.plot.group has a number (may need to merge to get zeros): 270 rows
8. Get the group mean for burned: end up with 2 means for each of 15 years: 30 rows
9. Get the group mean for control: end up with 2 means for each of 15 years: 30 rows
10. 60 rows total

Warner Creek, year 14 (Brown et al. 2013)

1. 8 3m x 3m subplots per plot. 11 plots in SF zone and 10 plots in WH zone
2. Mean species cover for SF zone, and WH zone
3. Assign species to groups, just use the 4 groups (ESH, ESS, FGH, FGS)
4. Sum species cover in each group: end up with 4 means for each zone: 8 rows

HJA, 15-44 years (Halpern and Lutz 2013)

1. 2m x 2m plots along transects. 132 plots in WS1 and 62 plots in WS3
2. Mean species cover for combined WS1 and WS3, 9 sample events
3. Data obtained from Halpern and Lutz 2013 supplemental appendix
4. Assign species to groups, just use the 4 groups (ESH, ESS, FGH, FGS)
5. Sum species cover in each group: end up with 4 means for each event: 36 rows

HJA, -4 to 17 years (Halpern and Franklin 1990)

1. Plot notes here
2. Data extracted (manually) from Halpern and Franklin 1990 Fig. 1
3. Group canopy cover (ESH, ESS, FGS)
4. Figure has FGH, but I don’t use because I don’t know if these include LSH
5. I’m assuming the classification did not change!
6. I changed -4 to -1 to get a mean of pre-disturbance for both watersheds (assuming the both -4 and -1 are similar pre-disturbance conditions.
7. I deleted years 8 and 14 for WS1
8. I combined years 16 and 17 and called it 16
9. After that there are 13 sample events: -1, 0, 1, 2, 3, 4, 5, 6, 7, 9, 11, 13, 16
10. 13 years * 3 groups = 39 rows

DEMO, years -1, 7, and 11 (Halpern et al. 2012)

1. Data provided by Charles Halpern
2. Plot notes here
3. Mean species cover by groups for each treatment and year

4. Data obtained directly from C. Halpern and he stated they were calculated:
5. For each group, sum species covers
6. Compute means of the 24 microplots
7. Compute means of all plots within plot type (cut, uncut, treatment)
8. Just use the 4 groups (ESH, ESS, FGH, FGS)
9. Just use these 5 treatments: 15% dispersed, 15% cut, 40% dispersed, 40% cut, 100% (control)
10. End up with 60 rows: 5 tx * 3 events * 4 groups

Tillamook, year 23 (actually an average of 17 to 29) (Baily and Poulton 1968)

1. Plot notes here
6. Mean species cover
7. Assign species to groups, just use the 4 groups (ESH, ESS, FGH, FGS)
8. Sum species cover in each group: end up with 4 means for each event: 4 rows