Forest Ecology and Management 324 (2014) 160–171

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Mark E. Swanson [a,*], Nichole M. Studevant [a], John L. Campbell [c], Daniel C. Donato [d]

[a] School of the Environment, Washington State University, Pullman, WA, United States
[c] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, United States
[d] School of Environmental and Forest Sciences, University of Washington, Seattle, WA, United States

ARTICLE INFO

Article history:
Available online 26 April 2014

Keywords:
Early-seral forest
Biodiversity
Legacy
Pacific Northwest
Pre-forest
Threatened and endangered species

ABSTRACT

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

1. Introduction

Naturally regenerating post-disturbance (early-seral) communities are increasingly recognized for their relevance to forest management, especially in landscapes where conservation of organisms, provision of habitat, non-timber forest products, and other ecosystem values are included in management objectives (Gobster, 2001; Swanson et al., 2011). In the Pacific Northwest (PNW) of the United States, ecosystem management on federal forest land is beginning to evolve from its recent emphasis on old-growth conservation toward managing for all characteristic seral stages, ranging from old-growth to structurally diverse early-seral (or pre-forest) communities (Franklin and Johnson, 2012). Defined as the successional stage occurring between a stand-replacing disturbance (including wildfire, wind, volcanic eruption, severe flood, and snow avalanche) and subsequent tree canopy closure (Swanson et al., 2011), naturally regenerating early-seral pre-forest communities are unique in being co-dominated by a wide range of plant forms including grasses, herbs, broadleaf shrubs, and hardwood and coniferous trees, and accompanied by the living and dead woody legacies of the pre-disturbance stand. These plant communities have been associated with a similarly diverse set of vertebrate and invertebrate animal taxa (Hammond and Miller, 1998; Hagar, 2007; Betts et al., 2010) and are often posited as the most species-diverse stage of forest succession (e.g., Franklin and Spies, 1991).

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

* Corresponding author. Tel.: +1 509 335 1349.
E-mail address: markswanson@wsu.edu (M.E. Swanson).

http://dx.doi.org/10.1016/j.foreco.2014.03.046
0378-1127/

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

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

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

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

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

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

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

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

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