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Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest

John L. Campbell [a,*], Daniel C. Donato [b]

[a] Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR, USA
[b] Washington State Department of Natural Resources, PO Box 47014, Olympia, WA, USA

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ABSTRACT

Both the structure and composition of naturally generated early-seral forests in the Pacific Northwest (PNW) can be profoundly different than that of more developed forest seres, especially in the period after a major disturbance but before conifers re-develop a closed canopy. While it is reasonable to suggest that the unique structure and composition of early-seral forests in the PNW give rise to equally unique functionality, identifying such linkages beyond that inferred by empirical observation is understandably difficult. To address this challenge, we explore the utility of a trait-based approach to identify the vegetation traits most strongly altered by canopy-opening disturbances (using wildfires as an example), and link these traits to secondary production and subsequent food webs. Preliminary analysis, based on original and literature-derived data, suggests that (1) Lepidoptera production, the primary prey base for forest birds in the PNW, is positively correlated with specific leaf area (SLA) which is higher in stands recently opened by canopy disturbance and (2) small mammal production, an important prey base for meso-predators, is positively correlated with SLA, which is higher in stands recently opened by canopy disturbance. These initial results lay the framework for linking disturbance type, disturbance severity, and subsequent successional pathways to trophic processes uniquely provided by the early-seral condition.

1. Introduction

Both the structure and composition of naturally generated early-seral forests in the Pacific Northwest (PNW) can be profoundly different than that of more developed forest seres, especially in the period following a stand-replacing disturbance but before conifers re-develop a closed canopy (see review by Swanson et al., 2011; Donato et al., 2012). Societal demands to accelerate forest succession following logging and natural disturbances in the last 70 years has rendered the early-seral condition structurally simplified and short-lived throughout much of the PNW (Hansen et al., 1991; Noss et al., 2006; Ohmann et al., 2007; Spies et al., 2007). Concerns that large portions of the PNW have become dominated by young, even-aged stands of Douglas-fir (*Pseudotsuga menziesii*) have prompted a variety of alternative silvicultural activities aimed at creating the structural heterogeneity believed to be important to the functionality of both old-growth and naturally-regenerating early-seral forests (Puettmann and Berger, 2006). However, as is the case with most restoration activities, it is difficult to determine to what degree such structural modifications will impart the desired functionalities, such as hydrological cycling, nutrient dynamics, and provision of wildlife habitat.

One solution to linking desired ecosystem-scale function to manageable forest structure is trait-based analysis (see Garnier et al., 2004; Garnier and Navas, 2012). Trait-based analysis is based on the axiom that the physical character and relative abundance of plant species influence ecosystem processes (Grime, 1998). Existing studies that compare forest function such as nutrient cycling, primary production, or wildlife use across discrete condition classes have provided direct empirical connections between management activities and functional outcomes, but a full understanding of how and why desirable ecosystem functions arise and are maintained could benefit hugely from trait-based approaches that more explicitly consider underlying physical drivers. Such approaches move beyond qualitative or discrete condition classes by scaling quantitative traits of individual plants (e.g., leaf nutrient content) to entire ecosystems by the relative abundance of those plants, then evaluating other aspects of ecosystem function along these continuous gradients. However, despite the growing popularity of trait-based approaches, they have rarely been applied to forest systems, and their utility in guiding forest management remains largely untested.

In this proof-of-concept paper, we explore the utility of a trait-based approach to identify the key vegetation traits strongly altered by canopy opening disturbances, and attempt to link these traits to secondary production and subsequent food webs. Our specific objectives are to:

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* Corresponding author. Tel.: +1 541 737 8426.
E-mail address: john.campbell@oregonstate.edu (J.L. Campbell).

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1. Identify a series of quantifiable plant attributes (traits) that may best distinguish the functionality of early (pre-canopy closure) seres from later closed-canopy, conifer-dominated seres in the PNW.
2. Evaluate changes in key plant traits during early succession in the PNW.
3. Explore the relationship between forest-wide leaf traits in the PNW and the arthropod and small mammal biomass they support.

2. Background

2.1. Food webs in early-seral forest: the knowledge gap

One of the most important yet elusive forest functions is the ability to support robust food webs and associated biodiversity. Wildlife diversity is regularly mentioned as one of the objectives of forest restoration, and robust food webs are often suggested as a major hallmark of early-seral forests (Swanson et al., 2011). Unfortunately, our understanding of forest food webs lags far behind that of aquatic systems. Most of what we know about wildlife in forests is based on animals' empirical affinity to certain habitats rather than their underlying trophic support systems.

It has been postulated that the growth and allocation patterns of plants occupying recently disturbed forests afford greater trophic transfer to herbivores than do plants that compose mature forests (Hansen et al., 1994; Hagar, 2007). Cross-biome comparisons by Cebrian (1999), ranging from aquatic ecosystems to grasslands to woody ecosystems, suggest that communities composed of tall-statured, long-lived plants pass a smaller fraction of their net primary production on to herbivores than do communities made up of short-statured, short-lived plants. Similar observations were made by McNaughton et al. (1989), who showed herbivory and secondary production to be positively related to net primary production (NPP) across biomes in a log–log manner, but with forests deviating from this pattern with less herbivory per unit NPP. The most attractive explanation for this pattern involves the ratio of metabolic to structural compounds. As eloquently articulated by Shurin et al. (2006), the tissues required to support and layer photosynthetic organs are simply less edible than a plant's metabolic tissues. Consequently, terrestrial ecosystems afford less trophic transfer than aquatic systems, and forests afford the least trophic transfer among terrestrial ecosystems.

Do these cross-biome patterns in trophic transfer apply also to forest successional states, which may differ dramatically in relative allocation to structural and metabolic tissue? Possibly, but the evidence to support this notion is scant. To begin with, energy transfer to herbivores in forests is typically so low (about one-half percent; McNaughton et al., 1989) that it often evades adequate quantification. Secondly, most all forest research performed on the early-seral condition has focused on its trajectory toward maturity and not the intrinsic nature of the early sere. In short, there are sound theoretical reasons to believe that early-seral forests promote unique and possibly larger food webs than do more advanced stages of forest development; especially in the PNW where environmental conditions favor succession toward a closed canopy of long-lived conifers. However, without a robust framework linking measurable plant functional traits to realized herbivore production, correlations between forest seral states and their animal associates will remain empirical at best and anecdotal at worst.

2.2. Understanding forest function through plant functional traits

Logically, the identity and relative abundance of plant species influence ecosystem processes. However, building a useful framework out of this axiom is challenged by the qualitative nature of plant identity (Vitousek et al., 1997; Chapin et al., 2000). Classifying plants into functional groups has proven useful (see Weiher et al., 1999; Grime, 2001, Westoby et al., 2002), but the most robust approach to date involves the quantitative scaling of specific functional traits from plant to ecosystem (see Lavorel and Garnier, 2002; Garnier et al., 2004; Lavorel, 2013).

Often referred to as functional trait analysis, this approach is based on Grime's (1998) biomass ratio hypothesis, which stipulates that one can scale quantitative traits of individual plants (suspected to be of functional significance) to the entire ecosystem by the relative biomass of plants having such traits. In essence, the biomass ratio hypothesis implies that ecosystem functioning is determined in large part by plant traits weighted by their relative dominance. Not surprisingly, the most useful plant traits are shown to be leaf characteristics such as leaf surface to volume ratios, leaf density, and leaf chemical content, in part because they are functionally coupled to ecosystem processes such as NPP, nutrient cycling, decomposition, and herbivory, but also because these leaf traits are associated with fundamental trade-offs between the acquisition and conservation of resources (Grime, 1979; Reich et al., 1992; Grime et al., 1997; Poorter and Garnier, 1999).

Secondary succession in forests of the PNW typically begins with the simultaneous establishment of ruderal forbs, broadleaf shrubs, and very long-lived conifers (Dyrness, 1973), structurally complemented by large volumes of dead and surviving legacy of the prior forest (Franklin et al., 2002). As a general rule, few species are lost or gained in these systems over successional time, rather species change in relative abundance as the initially dominant broadleaf shrubs and forbs become subordinate to conifer overstories (Halpern, 1989; Halpern and Spies, 1995; Kayes et al., 2010; Wimberly and Spies, 2001). While the exact structure and composition of early-seral forests in the PNW vary by factors such as disturbance type, disturbance severity, site productivity, and sivicultural intervention, the collection of live and dead plants that dominate early-seral forests do display some consistent traits that contrast with later stages of forest development. The purpose of this paper is to examine measurable traits of early-seral forests, consider their potential in supporting resource flow through food webs, and explore the utility of trait-based analysis in characterizing trophic functionality throughout forest succession in the PNW.

3. Postulating functional traits of early-seral forests in the PNW

Table 1 lists a number of measurable plant traits which are scalable to the ecosystem and may be particularly useful for quantifying changes in the functionality of PNW forests as they develop. Because the majority of herbivory in forests is provided through leaf production, leaf traits are among the most important in regulating secondary production. Leaf protein concentration, phenolic concentration, specific leaf area (SLA), and longevity all lend to higher leaf digestibility in early-seral forests dominated by shrubs and forbs compared to conifer-dominated mid-seral forests (Table 1). Co-variation among these leaf traits across taxa and biomes (driven by both allometric constraints and adaptive evolution) strengthens the connection between seral-specific life strategies and ecosystem provision for consumers (see Poorter et al., 2009). However, this co-variation does make it difficult to disentangle the relative importance of each specific leaf trait.

Reproductive traits such as the structure and production rates of flowers, fruits, and seeds have also proven valuable in inferring ecosystem function in some systems (Lavorel and Garnier, 2002). Certainly, the relative abundance of angiosperms in early-seral forests of the PNW affords a set of trophic pathways not fully provided by conifer-dominated seres. However, it remains unclear if