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

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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.
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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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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

Table 1
Scalable plant traits functionally relevant to trophic transfer in forest ecosystems

Plant trait (scalable to ecosystem using biomass ratio hypothesis)	Ecosystem function (process and examples of trait fostering trophic transfer in temperate forest ecosystems)	Ecosystem-average trait value in Pacific Northwest forests: Shrub-dominated early-seral	Conifer-dominated mid-seral
Leaf traits			
Protein concentration	High nitrogen demands of heterotrophic tissue growth explain forest herbivore preference toward leaves with high protein content (Mattson, 1980; Bryant et al., 1983)	High	Low
Polysaccarid:phenolic ratio	High digestible fraction promotes leaf herbivory	High	Low
Specific Leaf Area (SLA)	Thinner leaves afford higher gas exchange thus co-vary with above mentioned dimensions of digestibility (Wright et al., 2004). Herbivory of forest broadleaves 2-40 x that of conifers (Shaw et al., 2006; Keeling and Philips, 2007)	High	Low
Leaf turnover rate	The structural requirements and chemical defenses afforded longer-lived leaves render them less digestible than shorter-lived leaves (Colley et al., 1985; Matsuki and Koike, 2006); but see evidence to the contrary (Lowman, 1992)	High	Low
Reproductive traits			
Pollen and nectar	This high-energy food source is the sole trophic pathway for entire guilds of both vertebrate and non vertebrate obligate nectivores	High	Low
Fleshy fruit production	High-calorie and seasonally-important food source for many vertebrate consumers (Moegenburg and Levey, 2003; Kwit et al., 2004)	High	Low
Seed production	High-calorie and seasonally-important food source for many vertebrate consumers. Seed abundance correlated with mouse and small birds in early seral forests (Gashwiler, 1970)	High or low	High or low
Root traits			
Root turnover rate	Fine root turnover (reciprical to root size) contributes consumable biomass to rhizosphere and associated soil biota. Correlated with leaf production and soil heterotrophic respiration (Campbell et al., 2004a,b)	High	Low
Resprouting rate	Resprouting capacity affords rapid recovery of primary and secondary production following canopy-killing events (Fontiane, 2009; Donato et al., 2009). Strictly speaking only a promoter of other traits	High	Low
Stem traits			
Fractional allocation to stem	With stem wood being the least digestible of all plant tissues, greater allocation to leaves and fruit supports more herbivory	Low	High
Stature	Short stature plants afford more herbivory by ground-dwelling consumers (Shaw et al., 2006)	Low	High
Density (of dead wood at current decay state)	This trait is different from the others in that it quantifies a condition state rather than an adaptive trait. However since tree wood is consumed long after tree death, a forest's instantaneous capacity to support consumers depends on collective attributes of both live and dead plants. Dead wood density loss indicates transfer of energy to detritivores and fungal communities	High or low	High or low

angiosperm fruiting in early-seral forests transfers more or less primary production to consumers than does conifer seed production, which has been shown to be consumed at rates of up to 90% in the PNW (Gashwiler, 1970).

Because stems are rarely fed upon, their live traits have not been considered particularly important in driving trophic transfer. With respect to forests, however, two easily quantifiable stem metrics may be especially important in characterizing trophic transfer. The first of these is height. One of the most profound attributes distinguishing early-seral forests from later developmental stages is that aboveground production occurs at heights easily accessible by surface-dwelling herbivores. Does the average height of leaves, fruit, and seeds in mature forests protect them from consumption? Climbing rodents such as squirrels and specialized voles are not confined to any particular canopy strata and it is unlikely that the abundance of arthropod herbivores is height-dependent. Ungulate and lagomorph herbivory, however, is entirely dependent on canopy height, and mice activity is largely confined to the forest floor (Kaufman et al., 1985).

The second important stem trait is wood density, not so much of living wood, but that of dead wood as in indication of its decay status. Approximately one half of net primary production in PNW forests is spent building wood (Campbell et al., 2004a,b) and that which is not combusted or exported is eventually consumed by microbes and detritivores. All wood mass in a forest lies somewhere along a spectrum between live (highest density) and fully decomposed (lowest density), and the transfer of wood mass to decomposers and detrital consumers should be reflected by the collective average wood density. Just as the biomass ratio hypothesis applies to living structures, so should it apply to dead structure. Ecosystem-average wood density is easily assessed by scaling species- and decay class-specific wood densities (including live wood) across plot-level inventories of live and dead structures. The challenge will be to establish a useful relationship between wood density and the flux of past wood production through different decomposer communities.

The consideration of stem height and decay status as traits of functional significance does deviate somewhat from the traditional view of adaptive plant traits in that realized height and decay status are ontological rather than evolutionary. However, by including these metrics in forest trait analysis, we can capture much of the functional variation associated with growth, disturbance, and legacy structure, which, in the PNW, changes over time much more so than floristic composition (Wimberly and Spies, 2001).

4. Examples of changing traits through succession of PNW forests

4.1. Approach

After having identified specific leaf area (SLA) as among the most easily-measured and functionally-important ecosystem traits, we quantified early-successional trends in ecosystem-averaged SLA

for three different forest types in the PNW, each initiated by stand-replacing wildfire. Specifically, ecosystem-averaged SLA (defined as one-sided surface area of leaf per dry mass of leaf) was assessed for 11 study plots in the Pacific silver fir (*Abies amabilis*) forest association and 10 plots in the western hemlock (*Tsuga heterophylla*) forest association for 14 years following the 1991 Warner Creek Fire (using data reported by Brown et al., 2013), and in 8 plots in the Douglas-fir/tanoak (*Pseudotsuga menziesii/Lithocarpus densiflorus*) forest association for 10 years following the 2002 Biscuit fire (using original data following the methods of Donato et al., 2009). Ecosystem-averaged SLA was calculated as species-specific SLA weighted by each species' fractional contribution to total leaf area in a stand. Species-specific leaf area was calculated as field-assessed crown cover multiplied by a crown-form-specific estimate of Leaf Area Index (LAI). LAI = 7 for mature conifer canopy dominants, LAI = 4 for mature hardwood co-dominants, LAI = 1.5 for woody shrubs, and LAI = 1 for forbs (based on Campbell, unpublished data collected throughout the PNW, using methods described in Law et al., 2008). Values and sources of species-specific SLA, which ranged from 30 $cm^2\ g^{-1}$ for incense cedar (*Calocedrus decurrens*) to 305 $cm^2\ g^{-1}$ for vine maple *(Acer circinatum)* are provided in Appendix A.

4.2. Evaluation

Fig. 1 illustrates early-successional trends in ecosystem-averaged SLA for three different forest types in the PNW, each initiated by stand-replacing wildfire. Across these forests, ecosystem-averaged SLA was two to five times greater in the first year following wildfire than it was for neighboring mature forests (dashed horizontal line in Fig. 1), owing to a temporary shift towards thinner-leaved angiosperms and away from thicker-leaved conifers. Over time, increasing conifer establishment brings ecosystem-averaged SLA back toward pre-burned levels. Both the magnitude and rate of change vary across communities, reflecting the specific nature of succession at each site. The western hemlock forests, whose mature condition supports more conifer foliage than either the colder silver-fir forests or the dryer Douglas-fir/tanoak forests, experience the largest but shortest-lived successional pattern in SLA. The Douglas-fir/tanoak forest, whose mature condition includes a co-dominant class of broadleaf trees, experience the smallest but longest-lived successional pattern in SLA of those reported here. Moreover, the largely sclerophyllous (thick, leathery and evergreen) nature of resprouting shrubs in the Douglas-fir/tanoak forest means that the early-seral shift toward angiosperms results in smaller changes in ecosystem-wide SLA.

While these examples represent only a subset of PNW forests, and only a single disturbance agent, the simple observation that SLA follows a common trajectory, the variation of which is explainable in terms of basic site condition, suggests that SLA is a valuable metric to evaluate the functional response of these forests to disturbance and help characterize the unique nature of the early-seral condition.

5. Cases of consumer responses to early-seral traits

5.1. Approach

To investigate how the fraction of forest productivity transferred to food webs might vary with SLA, and the associated parameters of leaf digestibility that co-vary with SLA, we considered two existing studies of canopy arthropod and small mammal biomass whose data also afforded coincident assessments of forest SLA. To assess arthropod biomass as a function of host plant SLA, we used data reported by Schowalter and Zhang, 2005; Schowalter et al., 2005 collected from various locations throughout the western Cascades and northern Sierras. Arthropod abundance, originally reported as count by species per kilogram of vegetation sampled, was converted to biomass using genus-specific length and generalized mass-to-length insect allometry (Sage, 1982). Overall, 90% of the arthropod biomass reported was composed of folivores (largely Lepidoptera), with the remaining biomass equally represented by homopterans (sap-suckers), predators, and detritivores.

To assess small mammal biomass as a function of ecosystem-average SLA, we used data reported by Garman (2001) and Dodson et al. (2012). The data reported here all pertain to measurements conducted in the western hemlock forest association on mature forests originated from clearcut harvesting and subsequently subject to various levels of thinning designed to enhance structural complexity. Small mammal trapping was conducted for two years pre-treatment and three years post-treatment using a combination of Sherman live-traps and pit-fall traps designed to minimize variation in capture efficiency across treatments. We converted animal abundance, which was originally reported as individuals captured per trap night, to biomass captured per trap night using species-specific animal mass from Wilson and Carey (2000) and Reid (2006). Overall, small mammal biomass was approximately 70% Townsend's chipmunk (*Neotamias townsendii*), 20% Deer

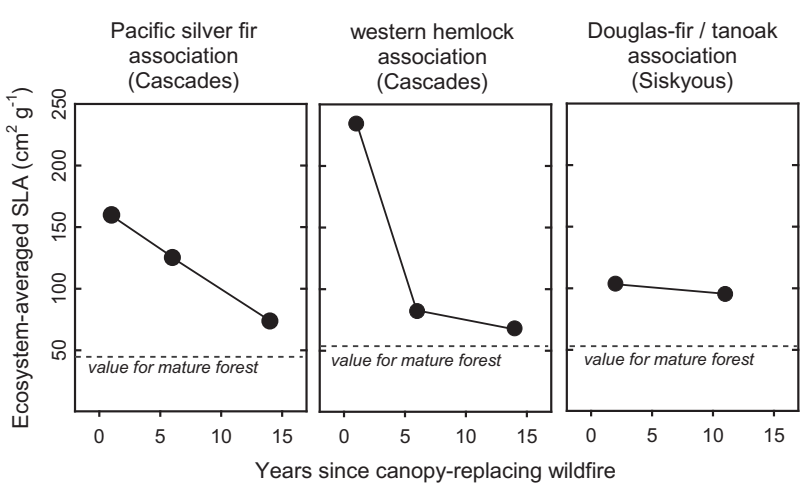

Fig. 1. Ecosystem-scaled SLA of early-seral forests initiated by high-severity wildfire. Circles are the average values among 10–12 replicate study plots. Dashed lines show the ecosystem-scaled SLA in neighboring undisturbed mature stands. Data for the Western hemlock and Pacific silver fir forests are from Brown et al. (2013). Data for the Douglas-fir/tanoak forests are original data for this study. SLA (Specific Leaf Area) is a measure of leaf area per unit leaf mass, which in the Pacific Northwest, is higher for angiosperm-dominated early-seral forests than for conifer-dominated mature forests.

mouse *(Peromyscus maniculatus)*, and 10% voles (*Arvicolinae*) and shrews (*Soricidae*). We converted associated vegetation data to ecosystem-average SLA using the species-specific values and sources given in Appendix A.

5.2. Evaluation

If it is the case, as we suggest above, that successional patterns in SLA affect the fraction of forest productivity transferred to herbivores and their subsequent predators, one may expect to see the ratio of animal biomass to plant biomass increase with increasing SLA and the associated parameters of leaf digestibility that co-vary with SLA. Of the two responses we evaluated (one involving canopy arthropods and one involving small mammals), both show significant relationships between consumer biomass and ecosystem-averaged SLA (Fig. 2).

In the case of small mammals, plot-level variation in ecosystem-averaged SLA resulted from vegetative response to various levels of thinning, designed to add structural complexity to even-aged conifer forests (Garman, 2001; Dodson et al., 2012). Small mammal biomass captured in these forests, as a fraction of total phytomass, increases dramatically with increasing SLA (Fig. 2). In the case of canopy arthropods, data published by Schowalter and Zhang (2005) and Schowalter et al. (2005) afforded direct comparison between arthropod biomass per unit plant biomass and the SLA of the host vegetation. As shown in Fig. 2, arthropod biomass tends to be higher when the SLA of the host tree is higher.

Due in part to the project-specific nature of animal capture rates, neither the small mammal nor arthropod biomass trends reported here are generically applicable to other forests. Still, these case studies amount to a proof of concept that leaf traits, measured at the individual level and scaled to the ecosystem, can capture the relative capacity for forests to support food webs over ranges experienced throughout forest succession in the PNW.

6. Conclusions

This first objective of this paper was to identify easily-measured vegetation attributes that would best distinguish the functionality of early-seral forests in the PNW from later-seral closed-canopy, conifer-dominated seres. Much like the trait-based analysis of other ecosystems (Garnier et al., 2004; Poorter et al., 2009; Navas et al., 2009), we suggest that leaf thickness, particularly SLA, is especially useful in quantifying potential herbivory rates during the early succession of PNW forests. This utility is because SLA is easily measured and scalable to the ecosystem. Furthermore, SLA co-varies with other structural and nutritional qualities, which together constitute the first principles of leaf digestibility (Reich et al., 1992; Wright et al., 2004; Poorter et al., 2009). New to previous trait-based analysis, we suggest that the density of all wood in a forest, whether dead or alive, should be included as a metric to evaluate functionality in early-seral forests. Just as Grime's (1998) biomass ratio hypothesis applies to living structures, so should it apply to dead structures. The volume of legacy wood present after disturbance is one of the primary axes of variation among early-seral forests in the PNW and its decay status directly reflects the trophic transfer of biomass to detrital and decomposer communities. As such, ecosystem-scaled measures of wood density (live and dead) represent an easily measured and functionally important trait. Finally, we suggest that canopy height be included in the trait analysis of early-seral forest, due to its role in concentrating consumable phytomass in strata reachable by a greater number of herbivores and its obvious relation to forest structural succession.

The second objective of this paper was to quantify early-successional changes in ecosystem-averaged SLA and compare them to levels expressed in neighboring mature seres. Variation in SLA across forest seres reflects early post-disturbance dominance by broadleaf angiosperms followed by the re-establishment of conifers. Similar successional trends in SLA have been reported for other regions by Garnier et al. (2004), Navas et al. (2009) and Campetella et al. (2011). Variations in SLA across forest associations reflect edapho-climatic differences in conifer growth rate and the relative abundance of sclerophyllous shrubs, whose SLA is intermediate between conifers and thin-leaved deciduous angiosperms. These general trends come as no surprise, given what we already know about the relative abundance of conifers versus broadleaves during early succession in the PNW; and it could be said that Fig. 1 amounts to commonly-acknowledged patterns in broadleaf abundance expressed in new units. However, even the simple re-expression of broadleaf abundance into SLA allows us to more precisely capture successional variation in leaf structure and theoretically brings us closer to the underlying mechanisms by which floristic composition may drive trophic transfer at the ecosystem scale. Furthermore, the five-fold variation in SLA we observed among forest seres means that this easily-measured and scalable axis of leaf structure has strong potential as a cross-site functional indicator in the PNW.

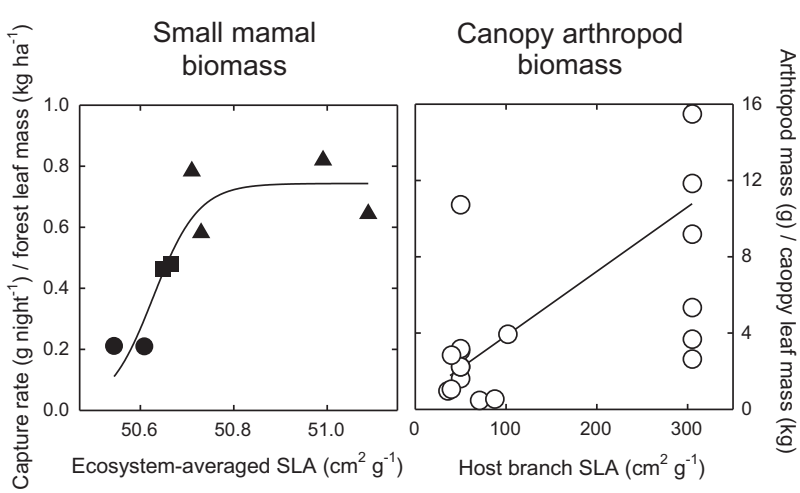

Fig. 2. Biomass of primary consumers per biomass of forest foliage as a function of SLA. Small mammal data are from Garman (2001) and Dodson et al. (2012) where variation in SLA arose from vegetation responses to prescribed canopy removal. Arthropod data are from Schowalter and Zhang (2005) and Schowalter et al. (2005) where variation in SLA resulted from stratified sampling of tree and shrub species. 2-parameter sigmoidal equation fits small mammal data with $R^2 = 0.83$ ($p < 0.001$); 2-parameter linear equation fits arthropod data with $R^2 = 0.34$ ($p < 0.01$).

The third objective of this paper was to explore the relationship between forest-wide leaf traits in the PNW and the arthropod and small mammal biomass they support. In both cases, the animal biomass supported per unit leaf biomass was positively and significantly correlated with leaf SLA. Again, it may be said that these trends amount to previously-established relationships between shrub and animal abundance in PNW forests (Sullivan, 1979; Corn et al., 1988; Hammond and Miller, 1998; Fontiane, 2009), and despite the theoretical relationship between SLA and foliar digestibility, the animal responses shown in Fig. 2 could be reflecting habitat affinity as much as actual trophic transfer. However, given the number of top-down factors that could cloud a detectable relationship between metrics of leaf digestibility and capturable consumer biomass, it is encouraging to see significant and sensible trends in the first two responses considered.

By itself, this analysis can neither quantify nor confirm functional connections between the structural attributes of early-seral forests and their particular capacity to support food webs. However, the patterns reported here prove the utility of trait analysis in characterizing trophic functionality throughout forest succession in the PNW. Further research must involve characterization of metrics beyond SLA across a much broader range of early-seral conditions. Due to the paucity of studies targeting the natural early-seral condition, an expansion of ground-based studies is warranted (Donato et al., 2012). Additionally many functionally-relevant metrics (including SLA, leaf longevity, live and dead wood density, and canopy height) could be computed from existing Forest Service inventory plots. Comparing the functional traits of targeted, rare, early-seral conditions to populations of inventory plots would go a long way toward understanding how unique, or potentially redundant, early-seral functions really are across the landscape. Regarding animal responses to vegetation traits, there are a number of existing studies (largely involving birds and small mammals) that have quantified animal abundance across discrete forest conditions (typically resulting from various management prescriptions). As done for the studies here, more data can be re-computed to reflect biomass as a function of continuous vegetation traits. In conclusion, this preliminary investigation lays a framework for linking disturbance type, disturbance severity, and subsequent successional pathways to trophic processes uniquely provided by the early-seral condition of PNW forests.

Acknowledgement

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Appendix A

See Table A1.

Table A1
Specific leaf area (SLA) for many tree and shrub species of the Pacific Northwest.

Species		Number of locations sampled	SLA (cm^2 of projected leaf area g^{-1} dry leaf mass)
Western juniper	(Juniperus occidentalis)	14	22.03
Shasta red fir	(Abies magnifica)	12	32.40
Grand fir	(Abies grandis)	1	33.20
Noble fir	(Abies procera)	1	33.81
Pacific silver fir	(Abies amabilis)	1	37.78
Greenleaf manzanita	(Arctostaphylos patula)	1	40.00
Mountain mohagany	(Cercocarpus ledifolius)	1	40.15
Engelman spruce	(Picea engelmannii)	9	40.75
Western redcedar	(Thuja plicata)	1	40.87
Subalpine fir	(Abies lasiocarpa)	7	45.29
White fir	(Abies concolor)	92	48.29
Canyon live oak	(Quercus chrysolepis)	9	57.06
Douglas-fir	(Pseudotsuga menziesii)	50	59.82
Sitka spruce	(Picea sitchensis)	1	60.50
Pacific rhododendron	(Rhododendron macrophyllum)	1	60.61
Snowbrush	(Ceanothus velutinus)	1	62.50
Mountain hemlock	(Tsuga mertensiana)	1	64.03
Golden chinkapin	(Castanopsis chrysophyll)	1	65.90
Tan oak	(Lithocarpus densiflora)	5	68.71
Pacific madrone	(Arbutus menziesii)	10	72.36
Ponderosa pine	(Pinus ponderosa)	82	79.63
Lodgepole pine	(Pinus contorta)	37	82.30
Sugar pine	(Pinus lambertiana)	6	98.04
Western white pine	(Pinus monticola)	11	104.39
Western larch	(Larix occidentalis)	11	109.27
California black oak	(Quercus kelloggii)	6	122.87
Red alder	(Alnus rubra)	1	144.02
Cascara buckthorn	(Rhamnus purshiana)	1	232.56
Bigleaf maple	(Acer macrophyllum)	2	232.82
Vine maple	(Acer circinatum)	1	305.34
Oregon white oak	(Quercus garryana)	2	321.31
Pacific dogwood	(Cornus nutallii)	2	371.08
Average non-pine needle-leafed conifer			44.02
Average sclerophyllous angiosperm			57.34
Average pine			91.09
Average non-sclerophyllous angiosperm			224.49

Samples were collected between 2001 and 2004 throughout Oregon, Washington, and Northern California. Live branch samples were collected from mid canopy positions, using a shotgun when necessary. SLA was determined by digitally scanning 5–100 individual fresh leaves (or needles) per branch sample and relating the subsequent oven-dry mass of the leaves (or needles) to the projected leaf area measured off the digital scan.

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