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

John L Campbell (Corresponding Author)

Department of Forest Ecosystems and Society

College of Forestry

Oregon State University

Corvallis, Oregon, USA

Email: john.campbell@oregonstate.edu

Phone: 1-541-737-8426

Daniel C Donato

Washington State Department of Natural Resources

PO Box 47014

Olympia, Washington, USA

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, 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.

Highlights

- Unique vegetative traits of naturally generated early-seral forests may support unique function
- Specific leaf area is higher among early-seral forests than for later seres
- Biomass of some primary consumers increase with increasing specific leaf area
- Functional trait analysis can link disturbance, seral state, and food webs in forests

Key words

59 Pacific Northwest, early-seral, trait analysis, herbivory, trophic transfer, food webs, post-
60 disturbance succession

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:

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, 1994; Hagar, 2007). Cross-biome comparisons by

123 Cebrian (1999), ranging from aquatic ecosystems to grasslands to woody ecosystems,

124 suggest that communities composed of tall-statured, long-lived plants pass a smaller

125 fraction of their net primary production on to herbivores than do communities made up

126 of short-statured, short-lived plants. Similar observations were made by McNaughton et

127 al. (1989), who showed herbivory and secondary production to be positively related to

128 net primary production (NPP) across biomes in a log-log manner, but with forests

129 deviating from this pattern with less herbivory per unit NPP. The most attractive

130 explanation for this pattern involves the ratio of metabolic to structural compounds. As

131 eloquently articulated by Shurin et al. (2005), the tissues required to support and layer

132 photosynthetic organs are simply less edible than a plant's metabolic tissues.

133 Consequently, terrestrial ecosystems afford less trophic transfer than aquatic systems,

134 and forests afford the least trophic transfer among terrestrial ecosystems.

135

136 Do these cross-biome patterns in trophic transfer apply also to forest successional

137 states, which may differ dramatically in relative allocation to structural and metabolic

138 tissue? Possibly, but the evidence to support this notion is scant. To begin with, energy

139 transfer to herbivores in forests is typically so low (about one-half percent; McNaughton

140 et al., 1989) that it often evades adequate quantification. Secondly, most all forest

141 research performed on the early-seral condition has focused on its trajectory toward

142 maturity and not the intrinsic nature of the early sere. In short, there are sound

143 theoretical reasons to believe that early-seral forests promote unique and possibly

144 larger food webs than do more advanced stages of forest development; especially in the

145 PNW where environmental conditions favor succession toward a closed canopy of long-

146 lived conifers. However, without a robust framework linking measurable plant functional

147 traits to realized herbivore production, correlations between forest seral states and their

148 animal associates will remain empirical at best and anecdotal at worst.

149

150 *2.2. Understanding forest function through plant functional traits*

151

152 Logically, the identity and relative abundance of plant species influence

153 ecosystem processes. However, building a useful framework out of this axiom is

154 challenged by the qualitative nature of plant identity (Vitousek and others 1997; Chapin

155 and others 2000). Classifying plants into functional groups has proven somewhat useful

156 (see Weiher et al., 1999; Grime, 2001; Westoby et al., 2002), but the most robust

157 approach to date involves the quantitative scaling of specific functional traits from plant

158 to ecosystem (see Lavorel and Garnier, 2002; Garnier et al., 2004; Lavorel, 2013).

159

160 Often referred to as functional trait analysis, this approach is based on Grime's (1998)

161 biomass ratio hypothesis, which stipulates that one can scale quantitative traits of

162 individual plants (suspected to be of functional significance) to the entire ecosystem by

163 the relative biomass of plants having such traits. In essence, the biomass ratio

164 hypothesis implies that ecosystem functioning is determined in large part by plant traits

165 weighted by their relative dominance. Not surprisingly, the most useful plant traits are

166 shown to be leaf characteristics such as leaf surface to volume ratios, leaf density, and

167 leaf chemical content, in part because they are functionally coupled to ecosystem

168 processes such as NPP, nutrient cycling, decomposition, and herbivory, but also

169 because these leaf traits are associated with fundamental trade-offs between the

170 acquisition and conservation of resources (Grime, 1979; Reiche et al., 1992; Grime et

171 al., 1997; Poorter and Garnier, 1999).

172

173 Secondary succession in forests of the PNW typically begins with the simultaneous

174 establishment of ruderal forbs, broadleaf shrubs, and very long-lived conifers (Dyrness,

175 1973), structurally complemented by large volumes of dead and surviving legacy of the

176 prior forest (Franklin et al., 2002). As a general rule, few species are lost or gained in

177 these systems over successional time, rather species change in relative abundance as

178 the initially dominant broadleaf shrubs and forbs become subordinate to conifer

179 overstories (Halpern, 1989; Halpern and Spies, 1995; Kayes et al., 2010; Wimberly and

180 Spies, 2001). While the exact structure and composition of early-seral forests in the

181 PNW vary by factors such as disturbance type, disturbance severity, site productivity,

182 and sivicultural intervention, the collection of live and dead plants that dominate early-

183 seral forests do display some consistent traits that contrast with later stages of forest

184 development. The purpose of this paper is to examine measurable traits of early-seral

185   forests, consider their potential in supporting resource flow through food webs, and

186   explore the utility of trait-based analysis in characterizing trophic functionality throughout

187   forest succession in the PNW.

188

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

190

191   Table 1 lists a number of measurable plant traits which are scalable to the

192   ecosystem and may be particularly useful for quantifying changes in the functionality of

193   PNW forests as they develop. Because the majority of herbivory in forests is provided

194   through leaf production, leaf traits are among the most important in regulating

195   secondary production. Leaf protein concentration, phenolic concentration, specific leaf

196   area (SLA), and longevity all lend to higher leaf digestibility in early-seral forests

197   dominated by shrubs and forbs compared to conifer-dominated mid-seral forests (Table

198   1). Co-variation among these leaf traits across taxa and biomes (driven by both

199   allometric constraints and adaptive evolution) strengthens the connection between

200   seral-specific life strategies and ecosystem provision for consumers (see Poorter et al.,

201   2009). However, this co-variation does make it difficult to disentangle the relative

202   importance of each specific leaf trait.

203

204   Reproductive traits such as the structure and production rates of flowers, fruits, and

205   seeds have also proven valuable in inferring ecosystem function in some systems

206   (Lavorel and Garnier, 2002). Certainly, the relative abundance of angiosperms in early-

207   seral forests of the PNW affords a set of trophic pathways not fully provided by conifer-

208   dominated seres. However, it remains unclear if angiosperm fruiting in early-seral

209   forests transfers more or less primary production to consumers than does conifer seed

210   production, which has been shown to be consumed at rates of up to 90% in the PNW

211   (Gashweiller, 1970).

212

213   Because stems are rarely fed upon, their live traits have not been considered

214   particularly important in driving trophic transfer. With respect to forests, however, two

215   easily quantifiable stem metrics may be especially important in characterizing trophic

216 transfer. The first of these is height. One of the most profound attributes distinguishing
217 early-seral forests from later developmental stages is that aboveground production
218 occurs at heights easily accessible by surface-dwelling herbivores. Does the average
219 height of leaves, fruit, and seeds in mature forests protect them from consumption?
220 Climbing rodents such as squirrels and specialized voles are not confined to any
221 particular canopy strata and it is unlikely that the abundance of arthropod herbivores is
222 height-dependent. Ungulate and lagomorph herbivory, however, is entirely dependent
223 on canopy height, and mice activity is largely confined to the forest floor (Kaufman et al.,
224 1985).
225
226 The second important stem trait is wood density, not so much of living wood, but that of
227 dead wood as in indication of its decay status. Approximately one half of net primary
228 production in PNW forests is spent building wood (Campbell et al., 2004) and that which
229 is not combusted or exported is eventually consumed by microbes and detritivores. All
230 wood mass in a forest lies somewhere along a spectrum between live (highest density)
231 and fully decomposed (lowest density), and the transfer of wood mass to decomposers
232 and detrital consumers should be reflected by the collective average wood density. Just
233 as the biomass ratio hypothesis applies to living structures, so should it apply to dead
234 structure. Ecosystem-average wood density is easily assessed by scaling species- and
235 decay class-specific wood densities (including live wood) across plot-level inventories of
236 live and dead structures. The challenge will be to establish a useful relationship
237 between wood density and the flux of past wood production through different
238 decomposer communities.
239
240 The consideration of stem height and decay status as traits of functional significance
241 does deviate somewhat from the traditional view of adaptive plant traits in that realized
242 height and decay status are ontological rather than evolutionary. However, by including
243 these metrics in forest trait analysis, we can capture much of the functional variation
244 associated with growth, disturbance, and legacy structure, which, in the PNW, changes
245 over time much more so than floristic composition (Wimberly and Spies 2001).
246

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^2g^{-1} for incense cedar (*Calocedrus decurrens*) to 305 cm^2g^{-1} for vine maple *(Acer circinatum)* are provided in Appendix A.

4.2. Evaluation

Figure 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 Figure 1), owing to a temporary shift towards thinner-leaved angiosperms and away

278   from thicker-leaved conifers. Over time, increasing conifer establishment brings
279   ecosystem-averaged SLA back toward pre-burned levels. Both the magnitude and rate
280   of change vary across communities, reflecting the specific nature of succession at each
281   site. The western hemlock forests, whose mature condition supports more conifer
282   foliage than either the colder silver-fir forests or the dryer Douglas-fir/tanoak forests,
283   experience the largest but shortest-lived successional pattern in SLA. The Douglas-
284   fir/tanoak forest, whose mature condition includes a co-dominant class of broadleaf
285   trees, experience the smallest but longest-lived successional pattern in SLA of those
286   reported here. Moreover, the largely sclerophyllous (thick, leathery, evergreen) nature of
287   resprouting shrubs in the Douglas-fir/tanoak forest means that the early-seral shift
288   toward angiosperms results in smaller changes in ecosystem-wide SLA.
289
290   While these examples represent only a subset of PNW forests, and only a single
291   disturbance agent, the simple observation that SLA follows a common trajectory, the
292   variation of which is explainable in terms of basic site condition, suggests that SLA is a
293   valuable metric to evaluate the functional response of these forests to disturbance and
294   help characterize the unique nature of the early-seral condition.
295

296   **5. Cases of consumer responses to early-seral traits**
297
298   *5.1. Approach*
299
300   To investigate how the fraction of forest productivity transferred to food webs might vary
301   with SLA, and the associated parameters of leaf digestibility that co-vary with SLA, we
302   considered two existing studies of canopy arthropod and small mammal biomass whose
303   data also afforded coincident assessments of forest SLA. To assess arthropod biomass
304   as a function of host plant SLA, we used data reported by Schowalter et al. (2005a and
305   2005b) collected from various locations throughout the western Cascades and northern
306   Sierras. Arthropod abundance, originally reported as count by species per kilogram of
307   vegetation sampled, was converted to biomass using genus-specific length and
308   generalized mass-to-length insect allometry (Sage, 1982). Overall, 90% of the arthropod

309 biomass reported was composed of folivores (largely Lepidoptera), with the remaining

310 biomass equally represented by homopterans (sap-suckers), predators, and

311 detritivores.

312

313 To assess small mammal biomass as a function of ecosystem-average SLA, we used

314 data reported by Garman (2001) and Dodson et al. (2012). The data reported here all

315 pertain to measurements conducted in the western hemlock forest association on

316 mature forests originated from clearcut harvesting and subsequently subject to various

317 levels of thinning designed to enhance structural complexity. Small mammal trapping

318 was conducted for two years pre-treatment and three years post-treatment using a

319 combination of Sherman live-traps and pit-fall traps designed to minimize variation in

320 capture efficiency across treatments. We converted animal abundance, which was

321 originally reported as individuals captured per trap night, to biomass captured per trap

322 night using species-specific animal mass from Wilson and Carey (2000) and Reid

323 (2006). Overall, small mammal biomass was approximately 70% Townsend's chipmunk

324 *(Neotamias townsendii)*, 20% Deer mouse *(Peromyscus maniculatus)*, and 10% voles

325 *(Arvicolinae)* and shrews *(Soricidae).* We converted associated vegetation data to

326 ecosystem-average SLA using the species-specific values and sources given in

327 Appendix A.

328

329 *5.2. Evaluation*

330

331   If it is the case, as we suggest above, that successional patterns in SLA affect

332 the fraction of forest productivity transferred to herbivores and their subsequent

333 predators, one may expect to see the ratio of animal biomass to plant biomass increase

334 with increasing SLA and the associated parameters of leaf digestibility that co-vary with

335 SLA. Of the two responses we evaluated (one involving canopy arthropods and one

336 involving small mammals), both show significant relationships between consumer

337 biomass and ecosystem-averaged SLA (Figure 2).

338

339   In the case of small mammals, plot-level variation in ecosystem-averaged SLA resulted

340   from vegetative response to various levels of thinning, designed to add structural

341   complexity to even-aged conifer forests (Garman, 2001; Dodson et al., 2012). Small

342   mammal biomass captured in these forests, as a fraction of total phytomass, increases

343   dramatically with increasing SLA (Figure 2). In the case of canopy arthropods, data

344   published by Schowalter et al. (2005a and 2005b) afforded direct comparison between

345   arthropod biomass per unit plant biomass and the SLA of the host vegetation. As shown

346   in Figure 2, arthropod biomass tends to be higher when the SLA of the host tree is

347   higher.

348

349   Due in part to the project-specific nature of animal capture rates, neither the small

350   mammal nor arthropod biomass trends reported here are generically applicable to other

351   forests. Still, these case studies amount to a proof of concept that leaf traits, measured

352   at the individual level and scaled to the ecosystem, can capture the relative capacity for

353   forests to support food webs over ranges experienced throughout forest succession in

354   the PNW.

355

356   **6. Conclusions**

357

358   This first objective of this paper was to identify easily-measured vegetation attributes

359   that would best distinguish the functionality of early-seral forests in the PNW from later-

360   seral closed-canopy, conifer-dominated seres. Much like the trait-based analysis of

361   other ecosystems (Garnier et al., 2004; Poorter et al., 2009; Navas et al., 2009), we

362   suggest that leaf thickness, particularly SLA, is especially useful in quantifying potential

363   herbivory rates during the early succession of PNW forests. This utility is because SLA

364   is easily measured and scalable to the ecosystem. Furthermore, SLA co-varies with

365   other structural and nutritional qualities, which together constitute the first principles of

366   leaf digestibility (Reiche et al., 1992; Wright et al., 2004; Poorter et al., 2009). New to

367   previous trait-based analysis, we suggest that the density of all wood in a forest,

368   whether dead or alive, should be included as a metric to evaluate functionality in early-

369   seral forests. Just as Grime's (1989) biomass ratio hypothesis applies to living

370 structures, so should it apply to dead structures. The volume of legacy wood present
371 after disturbance is one of the primary axes of variation among early-seral forests in the
372 PNW and its decay status directly reflects the trophic transfer of biomass to detrital and
373 decomposer communities. As such, ecosystem-scaled measures of wood density (live
374 and dead) represent an easily measured and functionally important trait. Finally, we
375 suggest that canopy height be included in the trait analysis of early-seral forest, due to
376 its role in concentrating consumable phytomass in strata reachable by a greater number
377 of herbivores and its obvious relation to forest structural succession.

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

398 The third objective of this paper was to explore the relationship between forest-wide leaf
399 traits in the PNW and the arthropod and small mammal biomass they support. In both
400 cases, the animal biomass supported per unit leaf biomass was positively and

401 significantly correlated with leaf SLA. Again, it may be said that these trends amount to
402 previously-established relationships between shrub and animal abundance in PNW
403 forests (Sullivan, 1979; Corn et al., 1988; Hammond and Miller, 1998; Fontaine, 2009),
404 and despite the theoretical relationship between SLA and foliar digestibility, the animal
405 responses shown in Figure 2 could be reflecting habitat affinity as much as actual
406 trophic transfer. However, given the number of top-down factors that could cloud a
407 detectable relationship between metrics of leaf digestibility and capturable consumer
408 biomass, it is encouraging to see significant and sensible trends in the first two
409 responses considered.
410
411 By itself, this analysis can neither quantify nor confirm functional connections between
412 the structural attributes of early-seral forests and their particular capacity to support food
413 webs. However, the patterns reported here prove the utility of trait analysis in
414 characterizing trophic functionality throughout forest succession in the PNW. Further
415 research must involve characterization of metrics beyond SLA across a much broader
416 range of early-seral conditions. Due to the paucity of studies targeting the natural early-
417 seral condition, an expansion of ground-based studies is warranted (Donato et al,
418 2012). Additionally many functionally-relevant metrics (including SLA, leaf longevity, live
419 and dead wood density, and canopy height) could be computed from existing Forest
420 Service inventory plots. Comparing the functional traits of targeted, rare, early-seral
421 conditions to populations of inventory plots would go a long way toward understanding
422 how unique, or potentially redundant, early-seral functions really are across the
423 landscape. Regarding animal responses to vegetation traits, there are a number of
424 existing studies (largely involving birds and small mammals) that have quantified animal
425 abundance across discrete forest conditions (typically resulting from various
426 management prescriptions). As done for the studies here, more data can be re-
427 computed to reflect biomass as a function of continuous vegetation traits. In conclusion,
428 this preliminary investigation lays a framework for linking disturbance type, disturbance
429 severity, and subsequent successional pathways to trophic processes uniquely provided
430 by the early-seral condition of PNW forests.
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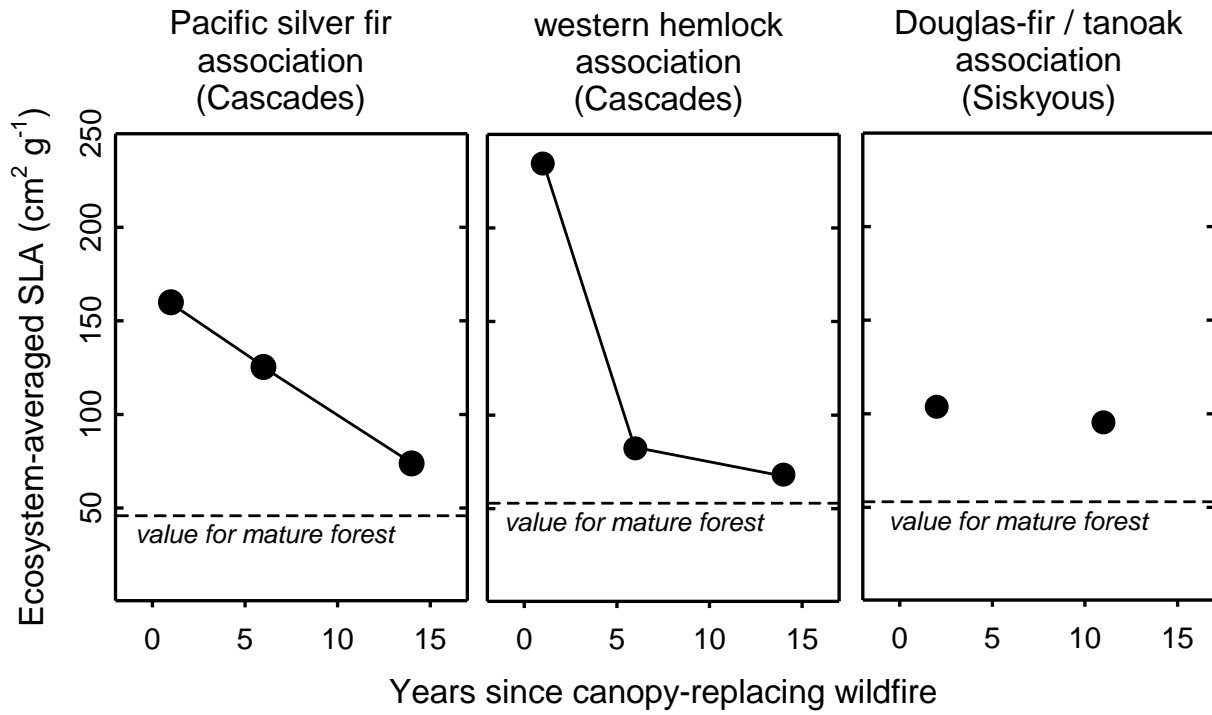617   spectrum. *Nature*. 428:821-827.

618

Figure captions

Figure 1. Ecosystem-scaled SLA of early-seral forests initiated by high-severity wildfire. Circles are the average values among 10 to 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.

Figure 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 Scholwater et al. (2005a and 2005b) 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).
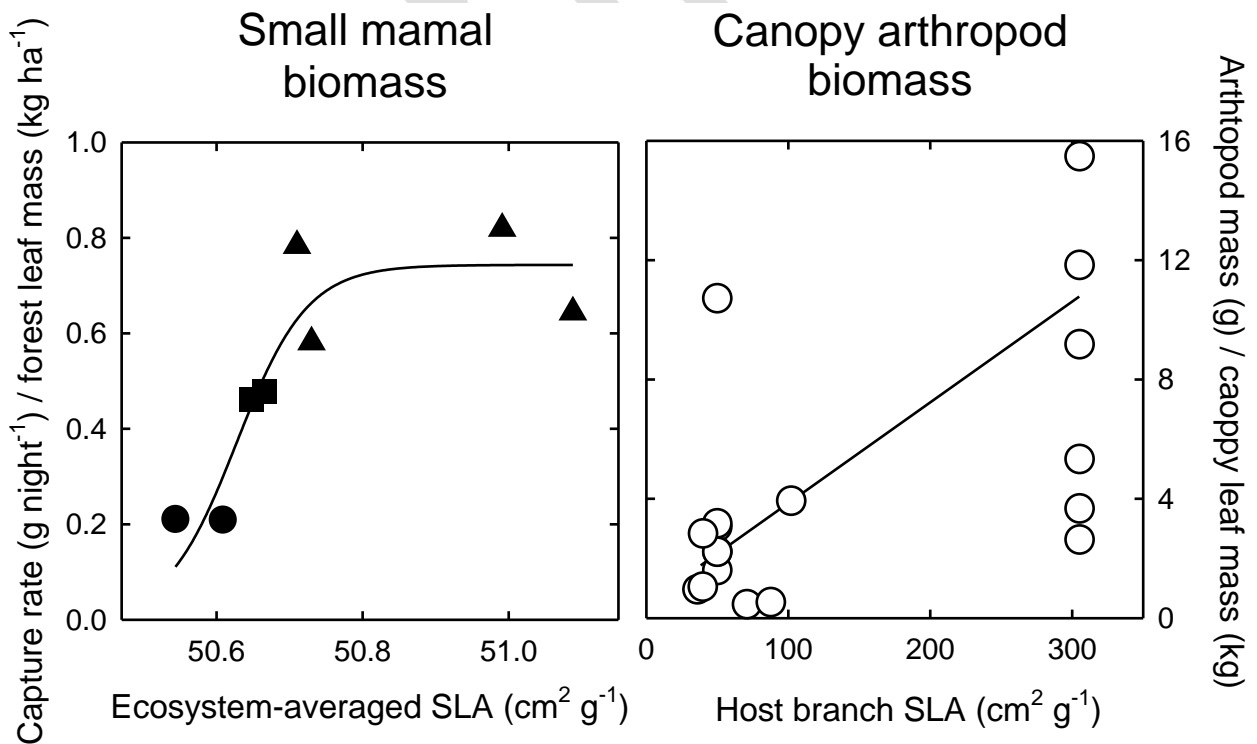
Table 1. Scalable plant traits functionally relevant to trophic transfer in forest ecosystems

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 (Coley et al. 1985; Matsuki, 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., 2004).	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

635 Figure 1

Pacific silver fir
association
(Cascades)

western hemlock
association
(Cascades)

Douglas-fir / tanoak
association
(Siskyous)

value for mature forest

value for mature forest

value for mature forest

Ecosystem-averaged SLA (cm^2 g^{-1})

Years since canopy-replacing wildfire

636

637 Figure 2

Small mamal
biomass

Canopy arthropod
biomass

Capture rate (g night^{-1}) / forest leaf mass (kg ha^{-1})

Ecosystem-averaged SLA (cm^2 g^{-1})

Host branch SLA (cm^2 g^{-1})

Arthopod mass (g) / caoppy leaf mass (kg)

638
639

Postulated energy transfer to food webs

intermediate *favoring detritivores*	highest *favoring both*
lowest *favoring neither*	intermediate *favoring herbivores*

wood density (live and dead combined) →

Specific Leaf Area →

Forest successional state in the Pacific Northwest

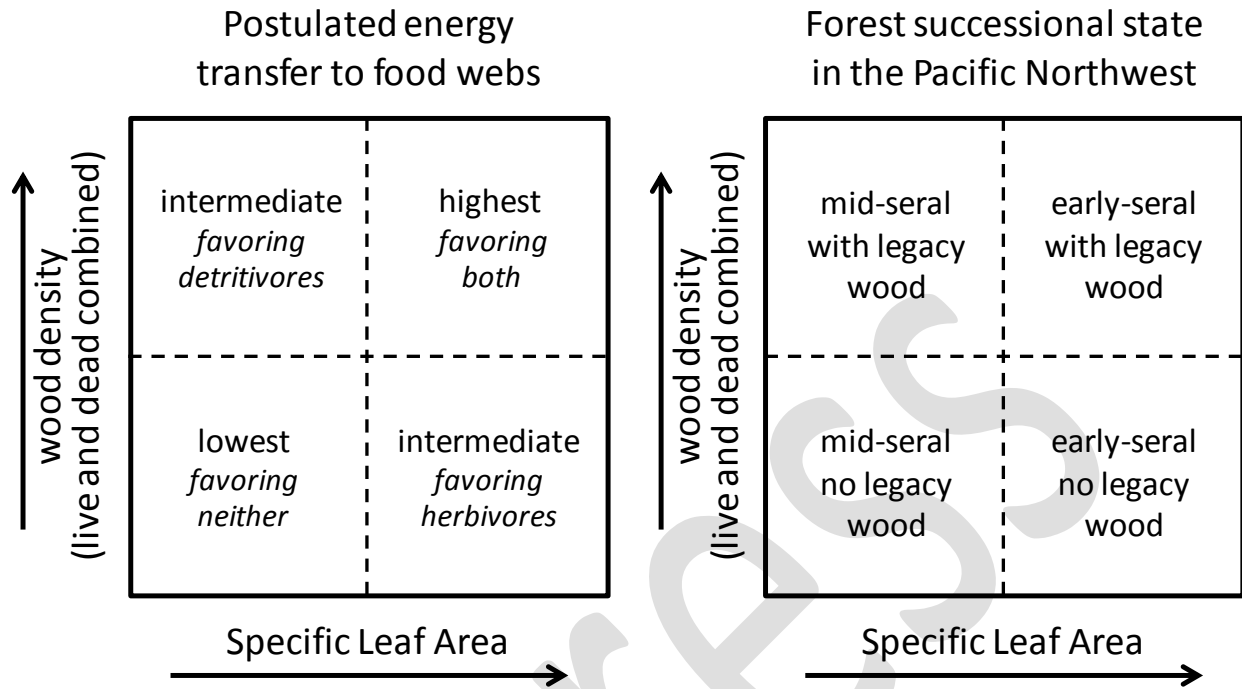|	
mid-seral with legacy wood	early-seral with legacy wood
mid-seral no legacy wood	early-seral no legacy wood

wood density (live and dead combined) →

Specific Leaf Area →

641

Appendix A. 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.