ARTICLE

Managing for adaptive capacity: thinning improves food availability for wildlife and insect pollinators under climate change conditions

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Abstract: A trait-based approach was developed to assess impacts of management practices on the adaptive capacity of ecosystems using impacts of overstory density and thinning on understory vegetation components related to wildlife habitat. The relationship between overstory basal area and understory vegetation for species grouped by traits that reflect food availability for wildlife (i.e., the production of flowers, fleshy fruit, and palatable leaves) was characterized in thinned and unthinned stands at seven Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in western Oregon 6 years following thinning. Lower overstory densities and thinnings were associated with a higher likelihood of selected ecosystem functions, specifically the provision of food for wildlife, as evident by higher cover of flowering, fleshy fruit and palatable leaf producing species. Within these functional groups, thinning increased cover of drought-, fire-, and heat-tolerant species, which suggests that these ecosystem functions are more likely to be maintained under climate change conditions. The responses of species groups appear to be driven by the sensitivity of species to resource availability and to physical disturbances associated with thinnings.

Résumé : Une approche fondée sur les traits fonctionnels des espèces végétales a été élaborée afin d'évaluer les impacts des pratiques d'aménagement sur la capacité des écosystèmes à s'adapter. À cette fin, nous avons eu recours à l'analyse des effets de la densité de l'étage dominant et de l'éclaircie sur les composantes de la végétation du sous-étage liées aux habitats fauniques. Dans un premier temps, les espèces du sous-étage de peuplements éclaircis depuis 6 ans et non éclaircis, dans sept forêts de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) de l'ouest de l'Oregon, ont été regroupées selon des traits qui reflètent la disponibilité de nourriture pour la faune (c.-à-d. la production de fleurs, de fruits charnus et de feuilles au goût agréable). Puis, la relation entre la surface terrière de l'étage dominant et les groupes d'espèces du sous-étage a été caractérisée. Les fonctions écosystémiques sélectionnées, particulièrement l'apport en nourriture pour la faune, avaient davantage de chances d'être associées aux étages dominants de densités plus faibles et à l'éclaircie. Ce résultat était prévisible étant donné le recouvrement plus élevé en espèces productrices de fleurs, de fruits charnus et de feuilles au goût agréable. Parmi ces groupes fonctionnels, l'éclaircie a conduit à l'augmentation du recouvrement en espèces résistantes à la sècheresse, au feu et à la chaleur, ce qui indique que ces fonctions écosystémiques seront vraisemblablement plus susceptibles d'être maintenues dans des conditions de changement climatique. Les groupes d'espèces semblent s'adapter selon la sensibilité des espèces à la disponibilité des ressources et aux perturbations physiques associées à l'éclaircie. [Traduit par la Rédaction]

Introduction

Forest management practices have mostly focused on increasing efficiency of growing and harvesting trees to achieve economic goals (Puettmann et al. 2009). Relative to historic conditions and in absence of natural disturbance events, these practices often led to simplified forest stand structure, composition, and function (Carey et al. 1999; Franklin 1993; Halpern and Spies 1995). In recognition of these effects, public sentiment shifted and management plans for many public forests now include a variety of objectives aimed to improve biological diversity and maintain ecological functions (Bengtsson et al. 2000). Great uncertainty associated with perturbations related to climate change has heightened concerns whether recent changes in forest resource management are sufficient to maintain desired ecosystem goods and services (Drever et al. 2006; Puettmann 2011).

With decreased financial resources and increased public scrutiny, foresters can benefit from management practices that increase the ecosystems' ability to adapt to novel, unexpected conditions (Folke et al. 2002; Puettmann 2011). Adaptive capacity of ecosystems is not necessarily organized around individual species, but rather by the amount and diversity of plant traits (Keddy 1992). For example, even though a species' contribution to an ecosystem function may decline, the specific ecosystem function may be maintained or increased if other species with similar traits are less sensitive and can compensate to maintain that ecosystem function (Allan et al. 2011; Walker 1995). Consequently, understanding how species with selected traits respond to changes can provide information about the likelihood that ecosystem functions are maintained under new, altered conditions (Boulangeat et al. 2012; Elmqvist et al. 2003; Walker 1995).

The scope of forest management practices such as thinning recently expanded beyond economic goals to promote and maintain heterogeneous and variable stand structures (Bormann et al. 2007; Thomas et al. 2006). On public lands in the Pacific Northwest, USA, goals of such practices include accelerated development of stand structures typical of unmanaged, mature forests, often with the goal of improving wildlife habitat (Thompson et al. 2009). These practices, e.g., variable density thinning intermixed with gaps and leave islands, lead to small-scale variability of resource availability, microclimate, physical disturbances, and competitive and facilitative interactions between overstory and understory plant communities (Fahey and Puettmann 2008; Hale 2003; Roberts 2004). Thinning impacts have been linked to greater abundance of forest understory vegetation (Ares et al. 2010; Canham et al. 1990; Thomas et al. 1999), greater plant species richness (Ares et al. 2010; Chan et al. 2006; Reich et al. 2012;

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Fig. 1. Conceptual model of ecosystem adaptability as a basis for our research approach. As an example, this model describes the flow of objectives for the fleshy-fruited functional group in the top tier. The second tier sorts species by similarity of response to specific disturbances, in this example, fire tolerance. The bottom tiers examine community characteristics and drivers responding to thinning and changes in cover. (Adapted from Puettmann (2011) with author's permission.)
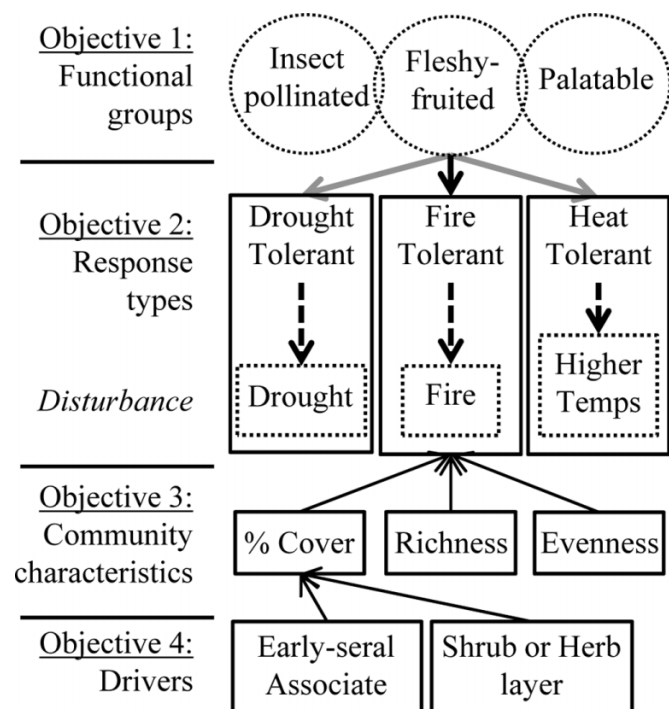
Thomas et al. 1999), increased abundance of shade-tolerant herbs (Alaback and Herman 1988; Bailey et al. 1998), and associated impacts on wildlife habitat. Initiatives to investigate whether forest management practices influence adaptability of forest functions to future climate conditions have started only recently (Cross et al. 2012).

Climate conditions in the Pacific Northwest are expected to increase by as much as 0.6 °C (1 °F) per decade, which is 0.4 °C (0.7 °F) per decade more than observed in the second half of the 20th century (Mote et al. 2008). Annual precipitation is expected to remain the same; however, winters are predicted to be wetter and summers drier, creating a greater likelihood of drought conditions (Mote et al. 2008). Strong relationships between climate and wildfire regimes likely result in larger, more frequent fires (Chmura et al. 2011). Changes in climate conditions are expected to impact the physiology, phenology, and disturbance regimes that influence abundance and distribution of individual species and, in turn, ecological functions (Bellard et al. 2012). Consequently, foresters must understand whether impacts of thinning on understory vegetation are maintained under altered climate conditions. This study utilizes a conceptual framework adapted from Puettmann (2011). This framework focuses on a nested set of traits and attributes that determine a species' contributions to ecosystem functions, as well as a species' response to changing conditions (Fig. 1) (Folke et al. 2010). A functional group (top tier in Fig. 1) includes all species that perform the same ecosystem function. Response-type groups (second tier in Fig. 1) include all species within specific functional groups that respond similarly to a given disturbance or change in environmental conditions (Elmqvist et al. 2003). Assessing thinning impacts on functional and response-type groups can provide an indication of whether thinning increases the likelihood that the selected ecosystems

functions are maintained under changing climate conditions (Grime 1998; Norberg and Cumming 2008; Puettmann 2011).

We are assessing the usefulness of this new, trait-based approach to evaluate effects of forest thinning on specific wildlife habitat functions and the potential provision of these functions under climate change conditions. Our overall goal was to investigate whether in the short term (6 years after harvest), thinning increases the likelihood that selected components of wildlife habitat quality can be maintained under climate change conditions. First, we tested how species that contribute to wildlife forage (three functional groups including fleshy-fruited species, insect-pollinated species, or species with palatable foliage) respond to thinnings. Second, within these functional groups, we developed subsets of species (response-type groups) that are tolerant to drought, fire, and increased temperatures and investigated how these species are impacted by thinnings. Third, we investigated community-level characteristics (i.e., richness and evenness) that may be reflective of patterns found in the responses of functional and response-type group to thinning presented in the first and second objectives. Fourth, we examined whether a subset of species, including early seral species or selected structural components (i.e., herbs and shrubs; bottom tier of Fig. 1), were mostly responsible for patterns found in response-types groups.

Methods

Study areas and design

This research was conducted as a component of the Density Management Study (DMS) (Cissel et al. 2006). The DMS includes seven thinning sites comprising 50- to 80-year-old planted and naturally regenerated Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands at low elevation in the Cascade and Coast ranges of western Oregon (Table 1). In addition to Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) and several hardwood species are minor components at some sites.

Four treatments were imposed: (1) unthinned control (CON), with 500–800 trees·ha⁻¹; (2) high-density retention (HD), with 300 trees·ha⁻¹; (3) moderate-density retention (MD), with 200 trees·ha⁻¹; and (4) variable-density retention (VD), with three subtreatments of 100, 200, and 300 trees·ha⁻¹, which were treated separately in the analysis. A portion of the area in HD, MD, and VD treatment units was left unthinned in circular 0.1, 0.2, and 0.4 ha leave island reserves. Similarly, a portion of the area in MD and VD treatment units was cut in circular 0.1, 0.2, and 0.4 ha patch openings. Sites were treated between 1998 and 2000. Stand history, site characteristics, and information about thinning operations are summarized in Table 1 (for more detail, see Cissel et al. 2006).

Data collection

Vegetation was monitored using a nested sampling design. Overstory attributes were monitored using circular 0.1 ha plots randomly positioned within treatments. Understory vegetation was measured using four 0.002 ha circular understory vegetation subplots per 0.1 ha overstory plot. These subplots were established 9 m from the overstory plot center in cardinal directions. Fourteen plots were placed in CON and 21 in HD, MD, and VD treatments. Overstory plots were located at least 15 m from other plots and treatment boundaries. Because one plot could not be located, only 76 plots were surveyed in the MD treatment at Bottomline.

Data were collected six years after thinning in June to September. Plot data included diameter at breast height (DBH) of live trees ≥5.1 cm DBH, which was used to calculate overstory basal area (m²·ha⁻¹). Topographic attributes included percent slope, aspect (degree), and elevation (m). Understory subplot data included percent cover of understory vegetation by species by visual estimation using cover classes of 1%, 5%, and 10% in 10% increments to 100%. Taxonomic classifications use the USDA PLANTS Database (USDA-NRCS 2010).

Table 1. Characteristics and stand history information of the Density Management Study sites. Additional information can be found in Cissel et al. (2006).

	Bottomline Coast Range	Delph Creek Cascade Range	Green Peak Coast Range	Keel Mountain Cascade Range	North Soup Coast Range	OM Hubbard Coast Range	Ten High Coast Range
Ecological province							
Latitude (N)	43°46′20.0″	45°15′56.0″	44°22′00.0″	44°31′41.0″	43°33′57.0″	43°17′30.0″	44°16′50.0″
Longitude (W)	123°14′11.0″	122°09′33.0″	123°27′30.0″	122°37′55.0″	123°46′38.0″	123°35′00.0″	123°31′06.0″
BLM district	Eugene	Salem	Salem	Salem	Coos Bay	Roseburg	Eugene
Resource area	Siuslaw	Cascades	Marys Peak	Cascades	Umpqua	Swiftwater	Siuslaw
County	Douglas	Clackamas	Benton	Linn	Douglas	Douglas	Lane, Benton
Total hectares	121.3	121	104.5	128.2	94.3	99.6	131.1
Slope (%)[a]	8–42	0–60	0 to >60	3–35	0–60	3–87	0 to >60
Elevation (m)[a]	236–369	557–721	472–765	617–768	159–411	436–783	384–870
Harvest date	September 1997	April 2000	January 2000	December 1997	August 1998	September 1997	April 1998 to March 2000
Stand age at harvest	55	53	56	44	48	39	44
Site index at year 50 (m) (King 1966)	42	37	37	39	40	36	38
Mean annual precipitation (mm)[b]	1299	1897	2121	1968	1735	1417	2726
Mean annual summertime maximum temperature (°C) 1994–2007[b]	26.8	23.6	26.1	23.9	25.5	24.8	25.1
Harvesting method[c]	HD: C	HD: C	HD: C	HD: C	HD: C	HD: C, G	HD: C
	MD: C	MD: G	MD: C, G	MD: G	MD: C	MD: C, G	MD: C
	VD: C	VD: G	VD: C	VD: G	VD: C	VD: C, G	VD: C
Management history[d]	None	PCT in 1974	None	PCT in 1964 and 1972	Fertilized	PCT in 1970, fertilized	PCT in 1972

[a]Slope and elevation data were collected at the overstory plot (0.1 ha) center.

[b]1994–2007 ClimateWNA, Center for Forestry Conservation Genetics, http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA_web/ [accessed 25 January 2011] (Wang et al. 2006).

[c]HD, high-density retention; MD, moderate-density retention; VD, variable-density retention. Harvesting method: C, cable; G, ground.

[d]PCT, precommercial thinning.

Species traits and attributes

Observed species were classified according to traits putatively associated with a species' ability to contribute to selected ecosystem functions and to respond to specific changes in environmental conditions. Primary sources for this included the USDA PLANTS Database (USDA-NRCS 2010) and the USDA Forest Service Fire Effects Information System (FEIS) Database (USDA Forest Service 2010). Other sources included online floras (Natureserve 2010; The Calflora Database 2010), regional plant guides (Gilkey and Dennis 2001; Hitchcock and Cronquist 2001; Pojar and Mackinnon 1994), scientific papers (Cates and Orians 1975), and personal observations.[1] When trait or classification data were lacking for a species, information from similar species or varieties was considered as a potential comparison, otherwise traits were labeled unknown. When plants were identified only to genus or growth form (i.e., grass, forb, fern, or shrub), information of the genus or growth form was used instead. In general, a majority of the vegetation cover was accounted for by species with information about the selected traits.

Species characterized as early seral associates in previous studies (Halpern and Spies 1995) and the FEIS Database (USDA Forest Service 2010) were used as representatives of early seral species. Herb species include forbs and grasses. Two tall ferns, i.e., *Polystichum munitum* [Kaulfuss] K. Presl and *Pteridium aquilinum* [L.] Kuhn, were included as shrub layer components due to their structural and functional roles in forest understories (Hagar et al. 2004).

The analytical approach was based on the mass-ratio hypothesis (Grime 1998; Lavorel 2013), i.e., increased cover of plants with specific traits or attributes implies increased number of flowers and biomass of fleshy fruits and palatable leaves. This assumption is supported by a variety of studies (see also Lavorel 2013). For example, percent cover has been shown to be correlated to plant biomass (MacDonald et al. 2012; Muukkonen et al. 2006), although the proportion of palatable biomass (i.e., leaves) related to herbaceous plants is generally greater than that of shrubs (Hanley et al. 2006). Furthermore, overstory removal not only increased cover of fruiting plants, but also increased the probability that understory plants flowered and produced fruit (Harrington et al. 2002; Huffman et al. 1994; Lindh 2008; Wender et al. 2004). Thinning also results in changes in leaf morphology (Beaudet and Messier 1998), an important factor influencing leaf palatability. A suite of plant traits, mechanisms, and interactions likely drives responses to drought, fires, and increased temperatures.

Functional groups

Fleshy-fruited species

Fleshy-fruited species include any plant species that produces a reproductive structure consisting of a fleshy, edible, pulp layer enclosing one or more seeds (Jordano 2000). Fruit types include aggregate, berry, drupe, drupelet, pepo, and pome. Additionally, strawberries (*Fragaria* sp. L.) are included here as fleshy fruits, which have a fleshy receptacle termed an accessory fruit. There has been no documentation of fleshy-fruit toxicity to wildlife in the study region; therefore, no fleshy-fruited species were excluded from the study.

Insect-pollinated species

Flowers contribute to food webs by feeding a variety of insects, which in turn feed a variety of predators such as insectivorous birds. A few plant species are primarily pollinated by birds, e.g., red-flowering current (*Ribes sanguineum* Pursh), gummy gooseberry (*Ribes lobbii* A. Gray), honeysuckle (*Lonicera* sp. L.), Columbia

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[1]Species characteristics and source information are summarized in Supplementary Table S1. Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2012-0345.

lily (*Lilium columbianum* Leichtlin), and western columbine (*Aquilegia formosa* Fisch. ex DC.). Based on the assumption that they are also pollinated by insects, these species are included in this functional group.

Palatable species

Palatability is contingent on several factors such as presence and abundance of secondary compounds, protein content, digestible energy, and the ratio of C to N (C:N) (Coley et al. 1985; Hanley et al. 2012). Information about species palatability was obtained from the USDA PLANTS Database (USDA-NRCS 2010) and the FEIS Database (USDA Forest Service 2010). For this study, species with either medium or high palatability ratings were classified as palatable.

Response types

Drought tolerance

The information is based on drought tolerance as classified by the USDA PLANTS Database (USDA-NRCS 2010). The database derives drought-tolerance ratings based on species physiographic occurrence in the regional landscape. For those species lacking drought-tolerance characterization in the USDA PLANTS Database or other regional floras, we considered the typical site characteristics to assign drought tolerance.

Fire tolerance

Sprouting species are generally able to regenerate quickly after disturbances such as fires. The capacity to re-sprout following death of aboveground structures was used as an indicator of a species fire tolerance and is categorized in the USDA PLANTS Database (USDA-NRCS 2010). For other life forms, a limited amount of sprouting information was found in the FEIS Database (USDA Forest Service 2010). Because much of the species information regarding re-sprouting was limited to shrubs, re-sprouting herbs are underrepresented in this response type. Other possible mechanisms that can confer fire tolerance, which include avoidance by completing the life cycle prior to the typical fire season, thick bark, and persistent seed banks, were not easily obtained for most species and consequently were not considered in the analysis.

Heat tolerance

We used the average summertime (June, July, and August) maximum temperature (T_{max}) for the warmest county in which a species was documented as a species index of heat tolerance. This information was derived from species distributions (USDA-NRCS 2010) and long-term climate data (Western Regional Climate Center 2007). T_{max} values ranged from 23.7 °C to 40.8 °C (median of 35.5 °C), suggesting that all species can persist under temperature increases greater than those predicted in the global climate models (GCMs) (maximum values of 7 °C by the 2080s; Mote et al. 2008). Species found in counties with a T_{max} higher than the overall median were designated as heat tolerant. This approach helps account for assumptions that (1) T_{max} of the three summer months is an indicator of survival in high temperatures (without considering moisture conditions), (2) T_{max} is uniform at the county level, regardless of variability in topography and local climate, and (3) in terms of heat tolerance, species are genetically homogeneous. This heat-tolerance index can only be viewed as an indicator of the likelihood that a species will persist in warmer temperatures relative to other species observed in this study. The ranges of absolute T_{max} values within the current range of all species included the predicted future temperature conditions on our study sites, suggesting that mortality or loss of a species due solely to higher temperatures is not very likely (data not shown). Thus, the index is to be viewed as an indicator of sensitivity that may only play out when other stressors predispose plants.

Fig. 2. Frequency distribution of plot overstory basal area showing the high amount of overlap of individual plots between treatments, despite distinct thinning targets. CON, control; HD, high-density retention; MD, moderate-density retention; VD300, VD200, and VD100, variable density retention to 300, 200, and 100 trees·ha⁻¹, respectively.
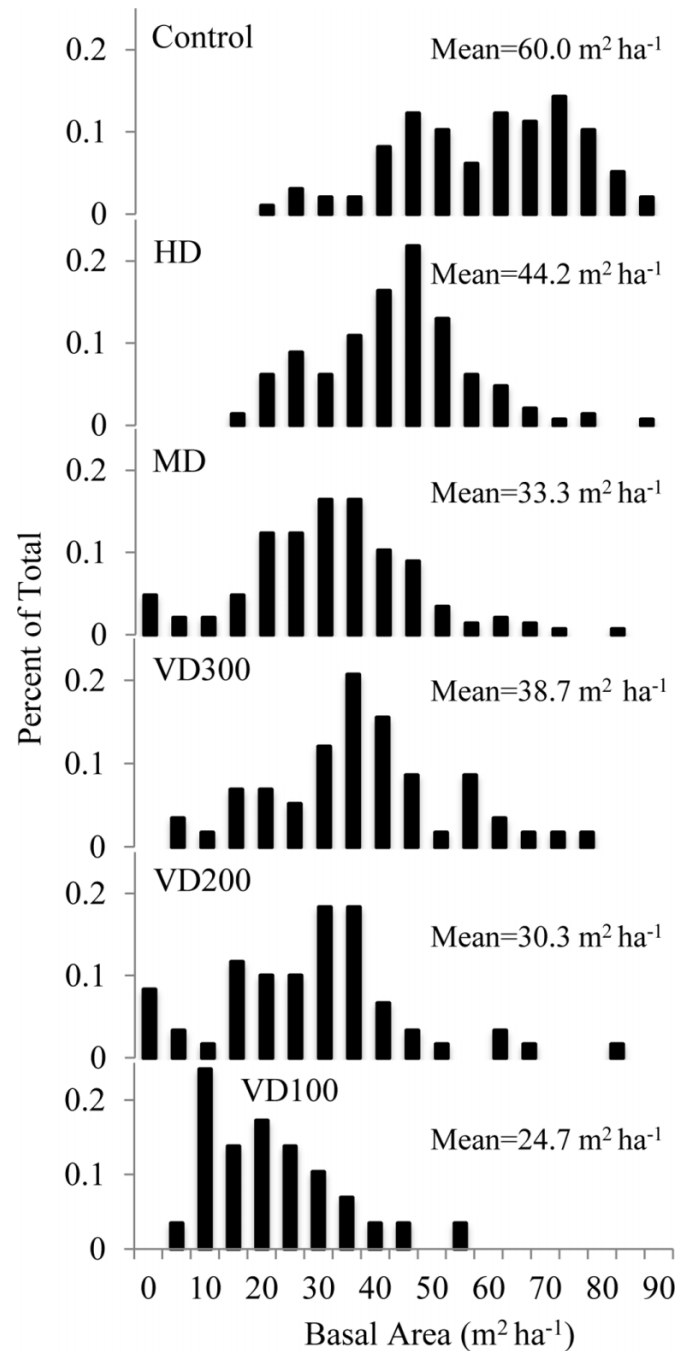
Analytical approach

Regression analysis was used to examine effects of overstory density (represented by basal area) and disturbance or thinning intensity (represented by thinning treatments) on cover, richness, and evenness of species groups. The wide range of overstory densities within and among treatments allowed for evaluation of influences of overstory density on understory vegetation (Fig. 2). The experimental design has a nested structure, i.e., subplots are located within plots, plots within treatment units, and treatment

Table 2. Dominant species (in terms of percent cover) and their functional and response-type groups (×, contributes to the functional group or response type; Unk, unknown contribution).

Scientific name	Common name	Mean cover when present (%)	Mean cover (%)	Frequency (n = 538)	Frequency rank	Functional group			Response-type group		
						Fleshy-fruited	Insect-pollinated	Palatable	Drought-tolerant	Fire-tolerant	Heat-tolerant
Polystichum munitum (Kaulf.) C. Presl	Western swordfern	15.61	15.20	0.97	1			×		×	
Gaultheria shallon Pursh	Salal	13.35	10.12	0.76	4	×	×			×	
Acer circinatum Pursh	Vinemaple	12.09	5.42	0.45	14		×	×		×	
Mahonia nervosa (Pursh) Nutt.	Oregon grape	6.49	4.34	0.67	8	×	×	×	×	×	
Pteridium aquilinum (L.) Kuhn	Western brackenfern	4.88	3.56	0.73	7				×	×	×
Oxalis oregana Nutt.	Redwood-sorrel	9.06	3.43	0.38	20		×	Unk	×	Unk	
Rubus ursinus Cham. & Schltdl.	Trailing blackberry	2.59	2.37	0.92	2	×	×	×	×	×	×
Corylus cornuta var. *californica* Marsh.	California hazel	7.82	2.03	0.26	31					×	
Vaccinium parvifolium Sm.	Red huckleberry	2.72	2.02	0.74	5	×	×	×	×	×	
Whipplea modesta Torr.	Common whipplea	5.17	1.68	0.33	23		×	Unk	×	Unk	

units within study sites, and warranted a mixed-effects model approach. Subplot values were averaged at plot level, and plot information was used in further analysis. The global model to describe Y_{ijk}, the mean functional-group cover, mean response-type cover, richness, or evenness was

$$Y_{ijk} = \beta_0 + \beta_1 I_1 + \beta_2 I_2 + \beta_3 I_3 + \beta_4 I_4 + \beta_5 I_5 + \beta_6 I_6 + \beta_7 x_k$$
$$+ \beta_8 x_k I_2 + \beta_9 x_k I_3 + \beta_{10} x_k I_4 + \beta_{11} x_k I_5 + \beta_{12} x_k I_6$$
$$+ \beta_{13} \text{slope} + \beta_{14} \text{aspect} + \beta_{15} \text{elev} + \lambda_i + \gamma_{ij} + \varepsilon_{ijk}$$

where β_0 is the fixed-effect intercept coefficient in controls; $\beta_1–\beta_6$ are fixed-effect coefficients associated with differences between treatments and controls; $I_1–I_6$ are indicators for treatment ($I = 1$ for corresponding treatment, $I = 0$ otherwise); β_7 is the fixed effect of the slope associated with basal area x of plot k; $\beta_8–\beta_{12}$ are fixed-effect coefficients for slopes of interactions between basal area and treatments; β_{13} is the fixed effect associated with percent slope of plot k; β_{14} is the fixed effect associated with aspect of plot k; β_{15} is the fixed effect associated with elevation of plot k; λ_i is the random effect of site; γ_{ij} is the random effect of treatment unit within site; ε_{ijk} is the random effect of plot within treatment unit within site; k, j, and i are the plot number ($k = 1$ to 77), treatment ($j = 1$ to 6), and site ($i = 1$ to 7), respectively; $\lambda_i \sim N(0, \sigma_\lambda^2)$ and $\text{Cov}(\beta_\lambda, \beta_{\lambda'}) = 0$, $\gamma_{ij} \sim N(0, \sigma_\gamma^2)$ and $\text{Cov}(\gamma_{ij}, \gamma_{i'j'}) = 0$, $\varepsilon_{ijk} \sim N(0, \sigma^2)$ and $\text{Cov}(\varepsilon_{ijk}, \varepsilon_{i'j'k'}) = 0$, and λ_i, γ_{ij}, and ε_{ijk} are all independent.

To obtain cover, we calculated the average cover of each species for each subplot and the total of average covers of all species that contribute to a group for each plot. Group cover can exceed 100% because of multiple vegetation layers. Layering likely reduces the correlation between shrub cover and biomass compared with the relationship between cover and biomass of herb layer species, which are generally shorter in stature, although this was not taken into consideration. Understory cover values excluded trees, regardless of size, and any shrub greater than 6 m tall. Plot species richness is the total number of species found in at least one of the

four understory subplots (species per 80 m²). To investigate whether dominant or minor species were more responsive, we quantified differences in species dominance using Pielou's evenness index, a measure of distribution of cover among species. This index was calculated for each plot (Pielou 1975), and plots with less than two species were omitted from this analysis because Pielou's evenness index could not be calculated.[2]

Fit of the global model for each response variable was assessed prior to model selection and regression analyses to ensure that assumptions of linear regression were met (Burnham and Anderson 2002), otherwise mean plot cover was log-transformed. When a functional or response type had no cover on at least one plot, data were log-transformed after adding 1 to each plot cover value. Co-linearity of potential explanatory variables was assessed using Pearson's correlation coefficients. Because of the absence of pretreatment data, we limited our analysis to species groups rather than individual species. The effects of slope (%), aspect (°), and elevation (m) were accounted for by including these variables in the model selection process. Aspect values were calculated as an absolute deviation from north, resulting in a 0°–180° linear scale (linasp; see Warren 2008).

Mixed-effects modeling was performed in R (version 2.13.2; R Development Core Team 2009) using the lme() function from the nlme package (Pinheiro et al. 2011). Correlation coefficients were derived in R using the cor() function from the stats package. Pielou's evenness index was calculated using the diversity() function from the vegan package.

Model selection

The Akaike information criterion corrected for small sample size (AIC$_c$) was used (Burnham and Anderson 2002). Models with the lowest AIC$_c$ values are considered to be best supported by the data (Akaike 1973). AIC$_c$ searches for the most parsimonious model, i.e., it rewards goodness of model fit and penalizes for additional parameters. In accordance with AIC$_c$ procedure, 25 models were developed representing four prior hypotheses,

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[2]The total number of plots used in the analyses of evenness for functional-group and response-type pairings are provided in Supplementary Tables S2.8, S2.9, and S2.10.

which assessed the importance of basal area (H1), treatment (H2), basal area by treatment interaction (H3), and differences due to slope, aspect, and elevation (H4). The null model (H0) is only a function of random effects associated with plot, treatment unit, and site, with no fixed effects. The null model was assessed to determine if overstory density influences are small and if other parameters not included in model selection, e.g., the spatial relationship of plots within treatments and sites, are more influential. Model fit is assessed by comparison of AIC_c values of each model with each other and the null model. Models with the lowest AIC_c have the highest support from the data, and delta values (Δ_i) provide an indication of the strength of evidence that a model is the best supported model in the set. Models with Δ_i values less than 2 are considered equivalent in fit (Burnham and Anderson 2002). The Akaike weight (w_i) is a measure of the probability that model i is the best supported model in the model set, with weights closest to 1 having the highest probability. Because AIC_c only provides a relative comparison of the models in the set, comparison with the null model provides an indication about the overall model fits. Models with AIC_c values lower than the null model suggest that variables not included in the models such as random change, genetic variability, or other stochastic factors are more important than measured factors.

AIC$_c$ analysis using the global model was used to select appropriate error structures. A full complement error structure (plots within treatments and sites) was best supported, or within, $\Delta_i < 3$ in all models and was used in subsequent analysis. Maximum likelihood and restricted maximum likelihood was used to generate AIC_c values and obtain regression coefficients, respectively. To evaluate the influence of the VD subtreatment of 100 trees·ha^{-1} (with the smallest number of plots), we evaluated the influence of the interaction term in models with and without inclusion of this VD subtreatment. If an interaction term was significant in both sets of models with the highest support, it was left in the model; otherwise it was removed.

Results

Overall, understory composition varied within and among sites. However, general trends of cover and richness of overall vegetation, as well as functional groups and response types, were similar 6 years after thinnings. More than 300 understory plant species were observed across all seven sites, with 94 to 169 species per site. However, most species contributing to the selected functions had relatively low abundance. The most abundant species in terms of mean plot cover and their associated functional and response-type groups are presented in Table 2. The figures presented herein are examples of the observed trends. Only CON and MD treatments are represented to provide contrast between thinned and unthinned stands, although the other treatments follow similar trends.[3]

Responses of functional and response-type groups

Lower overstory density and thinning were associated with greater likelihood of maintaining the functions of fleshy fruit production, insect pollination, and palatable forage production 6 years following thinning treatments. These relationships appeared to be consistent across ranges in slope, aspect, and elevation. Understory cover of functional groups generally increased along natural and thinning-induced gradients of decreasing overstory density. Models that included live tree basal area and thinning treatment were best supported by the data.[3] This suggested that in addition to lower densities, other factors associated with thinning such as harvesting disturbance are also influencing the understory vegetation community (Fig. 3). In contrast to MD and VD treatments, responses of understory vegetation to overstory

Fig. 3. Relationship of overstory basal area and mean total cover of (*a*) fleshy-fruited species, (*b*) insect-pollinated species, and (*c*) palatable species in the unthinned control and thinning treatments. CON, control; HD, high-density retention; MD, moderate-density retention; VD300, VD200, and VD100, variable density retention to 300, 200, and 100 trees·ha^{-1}, respectively. [a]Total cover of fleshy-fruited plants was log(Y + 1) transformed. [b]The best supported model did not distinguish between treatments for palatable species (see Supplementary Table S2.1).
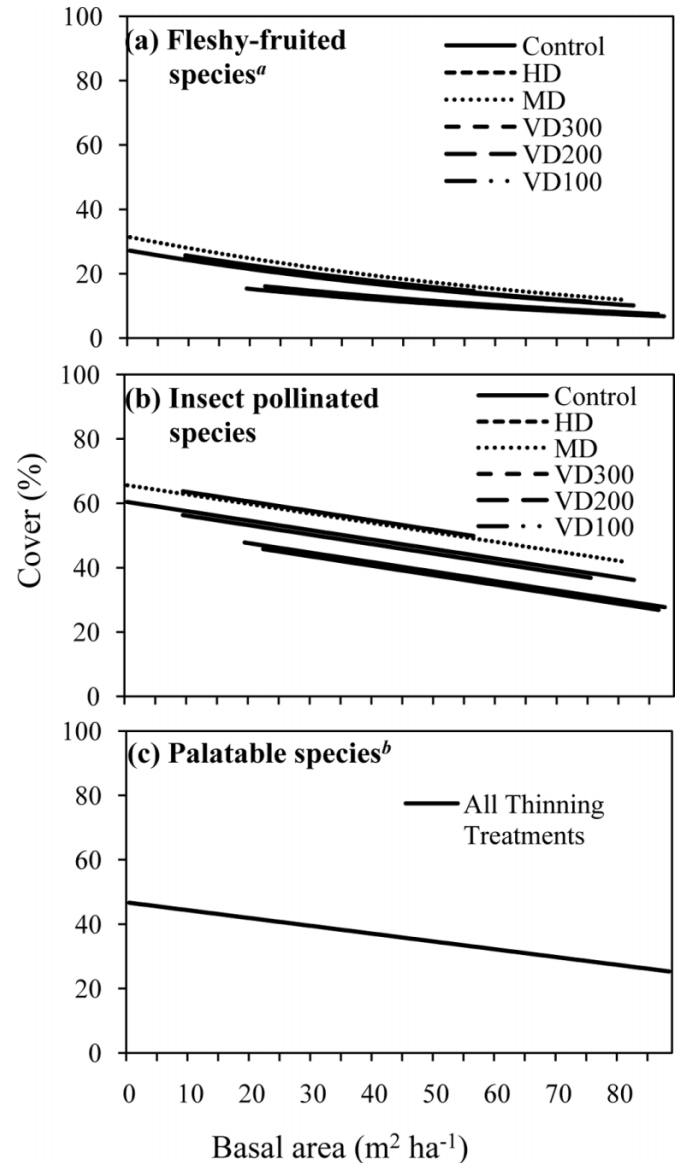

density in HD generally appear to be similar to unthinned controls in the fleshy-fruited and insect-pollinated functional groups. Cover of the palatable functional group was not strongly associated with treatments, indicating that palatable species cover was likely to increase with decreasing overstory density to a similar degree regardless of thinning treatments.

In general, the cover of all nine functional group – response type pairings increased with decreasing overstory density in thinned and unthinned stands. This indicates that the short-term response to thinning and lower overstory densities increased the

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[3]Estimates used to create the figures are presented in Supplementary Table S2.

Fig. 4. Insect-pollinated functional group and response type (*a* and *b*) cover, (*c* and *d*) richness, and (*e* and *f*) evenness along a basal area gradient for control (left column) and moderate-density treatments (right column). The null model was the best supported model for evenness of the drought-tolerant response type and was not plotted on the graph.
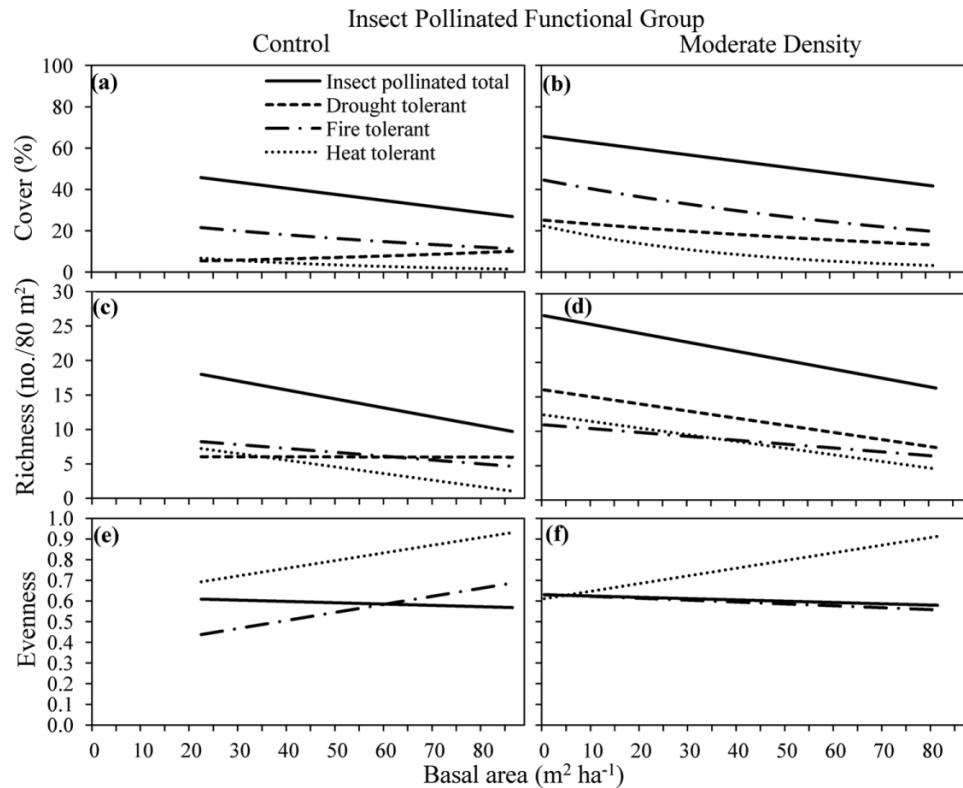
likelihood of maintaining the selected functions by increasing cover of drought-, fire-, and heat-tolerant species. However, drought-tolerant, insect-pollinated species were an exception. In unthinned stands, their cover decreased with lower overstory densities (Fig. 4*a*), whereas it increased in thinned stands (Fig. 4*b*). It must be noted that a model that did not distinguish between unthinned and thinned stands was similarly well supported by the data.[4] Cover of drought-tolerant species within the fleshy-fruited and palatable functional groups appear to respond less to lower overstory density compared with the overall response of understory vegetation (Figs. 5, 6*a*, and 6*b*).

Community characteristics and drivers impacting the probability of maintaining the selected functions

Thinning generally led to greater species richness of drought-, fire-, and heat-tolerant species within all three functional groups (Figs. 4, 5, 6*c*, and 6*d*). In unthinned stands (i.e., no thinning disturbance), species richness was higher in low-density conditions for eight of the nine functional group – response type pairings. For the exception, the drought-tolerant, insect-pollinated species, there was no change in species richness over the range of overstory densities in unthinned controls (Fig. 4*c*).

Changes in the rank distribution of species cover, as measured by Pielou's evenness index, were related to responses in plant cover of fire-tolerant and heat-tolerant functional group – response type pairings, but trends were variable (Figs. 4, 5, 6*e*, and 6*f*). Overstory density or thinning did not influence evenness of drought-tolerant species,[5] as dominant and minor species responded similarly. Patterns of evenness for heat-tolerant species are likely variable because they were influenced by the low species

cover (<5%) and richness (≤4 species) in all three functional groups, suggesting that this metric may not be informative for these functional group – response type pairings. Thinning and lower overstory density generally led to a less even distribution of cover among heat-tolerant species (e.g., Figs. 4, 5, 6*e*, and 6*f*), i.e., dominant species were more responsive than minor species. On closer examination, it appears that greater cover of one or a few dominant shrub species was generally responsible for the greater representation of heat-tolerant species at lower overstory densities in unthinned stands (e.g., Figs. 7*c*, 7*f*, and 7*i*), thereby decreasing evenness. On the other hand, thinning had a homogenizing effect on fire-tolerant species, where less dominant species had a greater response relative to dominant species (e.g., Figs. 4*f*, 5*f*, and 6*f*). In the unthinned stands, lower overstory density had the opposite effect on fire-tolerant, insect-pollinated, and fleshy-fruited species (Figs. 4*e* and 5*e*). In these groups, dominant species had a greater response in terms of increased cover relative to less dominant species, which is reflected in lower evenness values.

Greater cover of early seral species (e.g., *Rubus* sp. and *Holodiscus discolor* (Pursh) Maxim.) was a primary factor differentiating responses of understory cover in thinned and unthinned stands (e.g., Figs. 8*a*–8*f*). Early seral species tended to respond positively to thinning, i.e., the disturbance associated with thinning. Early seral species cover within response types was low (generally less than 2% cover) at high overstory densities and also under low overstory densities in unthinned stands for all nine functional group – response type pairings. In thinned stands, however, average cover of early seral species within response types reached more than 20% on plots with no overstory trees. The proportion of

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[4]Relevant model weights and Δ*i*s are presented in Supplementary Table S2.

[5]See Supplementary Tables S2.8, S2.9, and S2.10.

Fig. 5. Fleshy-fruited functional group and response type (*a* and *b*) cover, (*c* and *d*) richness, and (*e* and *f*) evenness as a function of overstory basal area for control (left column) and moderate-density treatments (right column). The null model was the best supported model for evenness of the drought-tolerant response type and was not plotted on the graph.
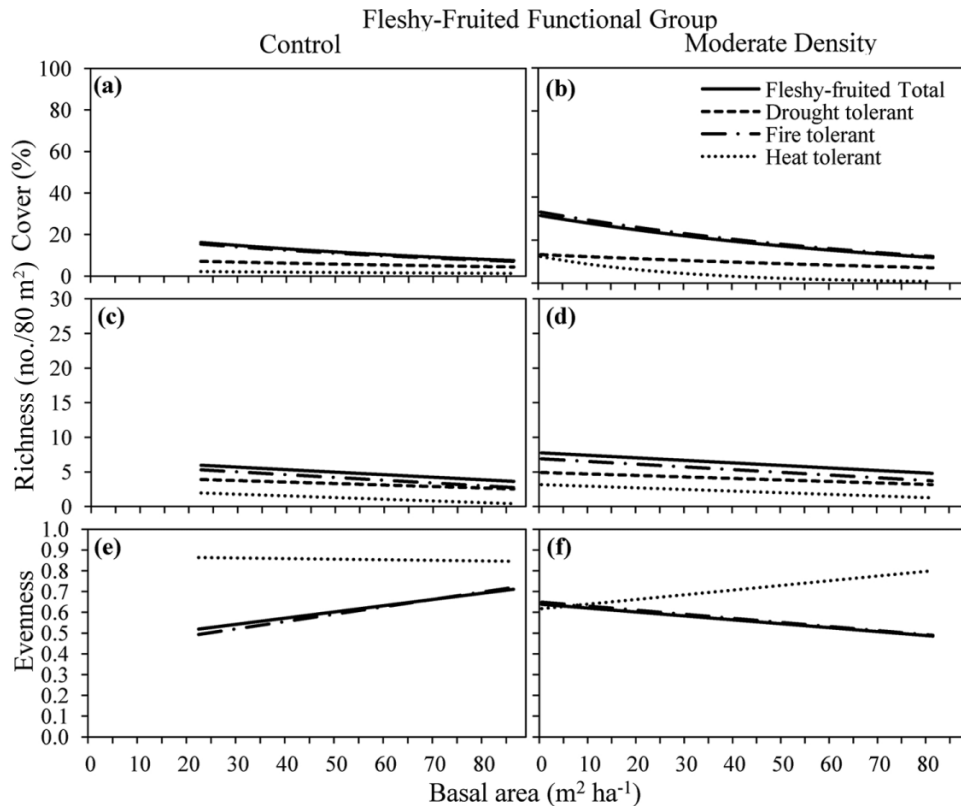
early seral species cover differed by response type. Early seral species accounted for 60% to 100% of the total cover of drought-tolerant and heat-tolerant response types at low overstory density for all functional groups. In contrast, early seral species only accounted for ~35% of the total cover of fire-tolerant species.

All functional group – response type pairings were dominated by species in the shrub layer (shrubs and ferns). These results may be somewhat biased towards shrubs, because information about functional trait and response characteristics was more likely to be available for these species, particularly in palatable and fire-tolerant – palatable groups. The palatable functional group was composed almost entirely of shrubs and ferns (see Figs. 7g–7i). In contrast, herbs were a minor component of the cover of all functional group – response type pairings (see Figs. 7a–7i). The insect-pollinated functional group had the highest contribution of the herb structural layer, although herb cover was less than 7% of total plot cover even at low overstory densities. Moreover, changes in overstory density or the thinning treatments appeared to have little effect on the herb layer (Figs. 7a–7i).

The impacts of overstory density and thinning on palatable species and fire-tolerant palatable species are similar, which is partially due to grouping schemes that were detailed above (Figs. 3c, 6a, and 6b). Cover values of fire-tolerant and palatable species groups were not influenced by disturbance associated with thinning treatments, suggesting that cover of these two groups was likely to increase with decreasing overstory density regardless of whether the stands had been thinned or not.

Management-sensitive models, which considered only the effects of treatment and live tree basal area, were not generally best supported by the data.[6] The deltas and weights for all of these

models predicting cover and evenness were greater than 4 and near or equal to zero, respectively, but these models generally had support greater than the null models. On the other hand, the distinction between best fitting and general management models was less when predicting species richness (Supplementary Table S3). The parameter estimates for best supported models and the null model are presented in Supplementary Table S2).

Discussion

The study results provide an example of the value and insights that can be gained by applying a conceptual model of ecosystem adaptability as a framework to assess impacts of forest management (Fig. 1) and gain insights as to how ecosystems adapt to perturbations such as climate change (Thompson et al. 2009). Separating species by their traits and attributes into functional and response-type groups facilitated a quantitative assessment of thinning impacts on potential adaptability of specific functions to specific perturbations (Folke et al. 2010). Our results and previous research suggest that management practices that lower overstory density will increase the amount of understory species that provide for wildlife forage and insect pollination. Furthermore, low overstory densities and thinnings were associated with a higher cover and greater diversity of selected response types that indicate that these functions are more likely maintained under climate change conditions. Our approach allows integration of the individualistic responses of understory species to future conditions in an analysis that quantifies the adaptive capacity of ecosystems (Suding et al. 2003). The results suggest that increased amount and species diversity within selected functional and response-type

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[6]See Supplementary Tables S2 and S3 for parameter estimates and AIC$_c$ statistics.

Fig. 6. Palatable functional group and response type (*a* and *b*) cover, (*c* and *d*) richness, and (*e* and *f*) evenness as a function of basal area for control (left column) and moderate-density treatments (right column). The null model was the best supported model for evenness of the drought-tolerant response type and was not plotted on the graph.
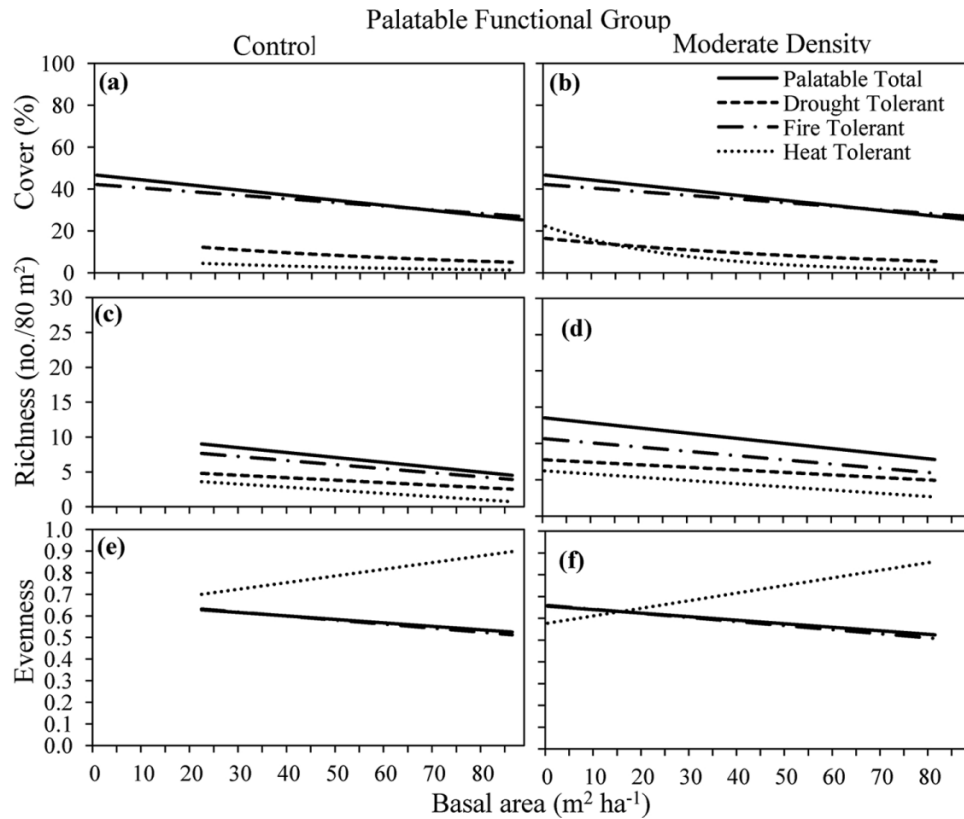
groups may confer greater adaptability to climate change in the short term. However, long-term trends are uncertain, as studies of understory composition multiple decades after thinning have shown inconsistent results (e.g., Lindh and Muir (2004) versus Bailey et al. (1998)).

Response patterns of the selected functional and response-type groups suggest that understanding functional and response traits can also aid in the understanding of underlying mechanisms. In our study, increases in cover and richness of understory vegetation were most prevalent. Impacts on evenness were variable or minor, suggesting that responses were not simply driven by rank–functional relationships (sensu Walker et al. 1999). The two mechanisms that may explain observed increases in cover and richness of understory vegetation with lower overstory density include (*i*) higher resource availability and (*ii*) physical disturbance to vegetation and forest floor (Gilliam and Roberts 2003; Odion and Sarr 2007; Thomas et al. 1999).

Influence of higher resource availability on understory vegetation

With lower overstory density, decreased resource utilization of overstory trees results in increased resource availability to understory vegetation (Hale 2003; McDowell et al. 2003; Thomas et al. 1999). However, greater abundance of hardwood species (e.g., red alder (*Alnus rubra* Bong.) in conifer stands can increase abundance of understory plants regardless of thinning intensity (Hanley et al. 2006). Depending on site and weather conditions, different resources such as light (e.g., Drever and Lertzman 2003), moisture (Harrington and Edwards 1999), or a combination (e.g., Drever and Lertzman 2001) may be limiting, and our study cannot distinguish among those. However, the limited responses of drought-tolerant response types in all three functional groups to lower overstory densities confirm that these species appeared to have low sensi-

tivity to limited availability of resources (Ninemets and Valladares 2006; Sack et al. 2003).

Greater resource availability following thinning can also have negative effects on species diversity, but this was not observed in our study. Release and expansion of one or more dominant species responding to greater resource availability can reduce species diversity through competitive exclusion or allelopathic interactions (Decocq et al. 2004; Grime 1973; Reich et al. 2012; Stewart 1975). Instead, recruitment of species following thinning generally appeared to have a homogenizing effect on species abundances within functional and response-type groups, with notable exceptions.

Influence of thinning disturbance on understory vegetation

Effects of thinnings not directly associated with overstory density such as physical impacts of harvesting operations due to residual slash or downed wood (Nelson and Halpern 2005) may also influence understory vegetation. Also, thinning often influences germination patterns by exposing mineral soil and seed germination substrate and affecting microsite conditions (Gray and Spies 1997; Roberts 2004; Roberts and Gilliam 1995).

Damage to understory vegetation through harvesting activities is especially evident for tall and sprouting vegetation (Chan et al. 2006; Davis and Puettmann 2009; Wilson and Puettmann 2007). For the functions considered in this study, the predominant species were mostly shrub layer species. Therefore, direct impacts of harvesting operations may have a larger and more persistent effect on the selected functional and response-type groups than herb layer species, and these effects may change over time. It is likely that as effects of harvesting disturbances decrease, the influence of post-thinning overstory recovery will increasingly shape patterns of understory vegetation, mainly by decreasing

Fig. 7. Cover of shrub and herb layers and total response-type group as a function of overstory basal area for (*a*, *b*, and *c*) insect pollinated, (*d*, *e*, and *f*) fleshy-fruited, and (*g*, *h*, and *i*) palatable functional groups in moderate-density treatments. The null model was the best supported model for herb layer cover of fleshy-fruited species and was not plotted on the graph.
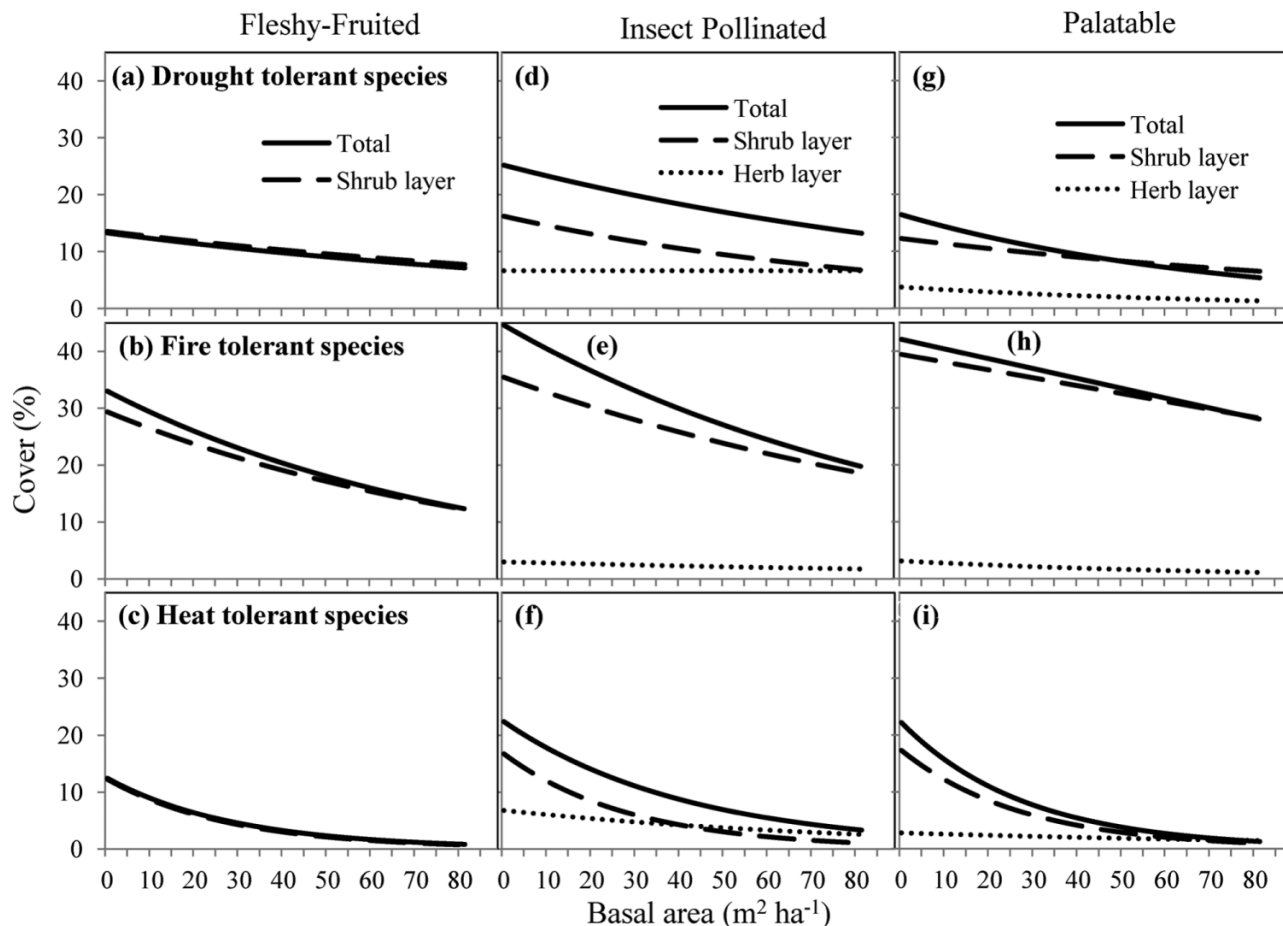
resource availability through increased competition from overstory trees (Lindh and Muir 2004).

Combined influence of resource availability and thinning disturbance on understory vegetation

Greater cover and richness of early seral species after disturbances such as thinnings were the primary drivers of treatment differences in the relationship between basal area and cover and richness of functional and response-type groups (Halpern 1989; Halpern and Spies 1995; Odion and Sarr 2007). This has been extensively documented for short-term responses (including Ares et al. (2009) using the same study sites), but longer term responses are harder to predict (e.g., Bailey et al. (1998) versus Lindh and Muir (2004)). The response of early seral vegetation may also explain the behavior of heat-tolerant response-type groups. Heat-tolerant species in our sample were basically all considered early seral (Pearson's correlation coefficient = 0.98). More open conditions such as those created by thinning result in higher variability in the extremes of ambient air and soil temperatures (Heithecker and Halpern 2006), thus benefiting species that can tolerate these extremes. It is likely that these conditions will change over time as overstory canopies close and shrub layer species recover from thinning operations. Thus, impacts of thinning on understory species groups will likely decrease over time, even though long-term thinning impacts have been documented (Bailey et al. 1998; Lindh and Muir 2004; Thysell and Carey 2000). Results from the same study using data collected 11 years following thinnings suggest that impacts of thinning on understory vegetation can be

sustained longer in lower density portions (Ares et al. (2010), see also Deal (2007) and Hanley et al. (2006)). However, overstory trees in these forests are very dynamic, and multiple thinnings may be required to maintain a high abundance of early seral species (Berger et al. 2012).

Influence of various thinning intensities on understory vegetation

A lack of response to low levels of thinning (HD) suggests that moderate to heavy thinning intensities may be required to generate increased cover of the insect-pollinated and fleshy-fruited functional groups and their response types. In contrast to the more intensive MD and VD treatments, the ground disturbance and other thinning impacts in the HD treatment may have been insufficient to induce or maintain changes in cover of understory vegetation 6 years after harvest. However, other studies have failed to discern differential responses of understory vegetation among different thinning intensities, at least in the short term (Ares et al. 2009; Davis and Puettmann 2009). Scale of observations (treatment average versus sampling plot), degree of overlap of individual plot overstory basal areas, and spatial variability in tree density (see Dodson et al. 2012) in the CON and HD treatment versus the other treatments may explain some of the inconsistencies of vegetation response among studies. The smaller scale used in this study is more aligned with the spatial scale of seedling–plant interactions (Wagner and Radosevich 1998) and thus may be a better reflection of spatial variability as it affects species cover and richness.

Fig. 8. Cover of early seral species and total response-type groups in (*a*, *c*, and *e*) controls and (*b*, *d*, and *f*) moderate-density treatments along a basal area gradient for the insect-pollinated functional group (fleshy-fruited and palatable functional groups not shown).
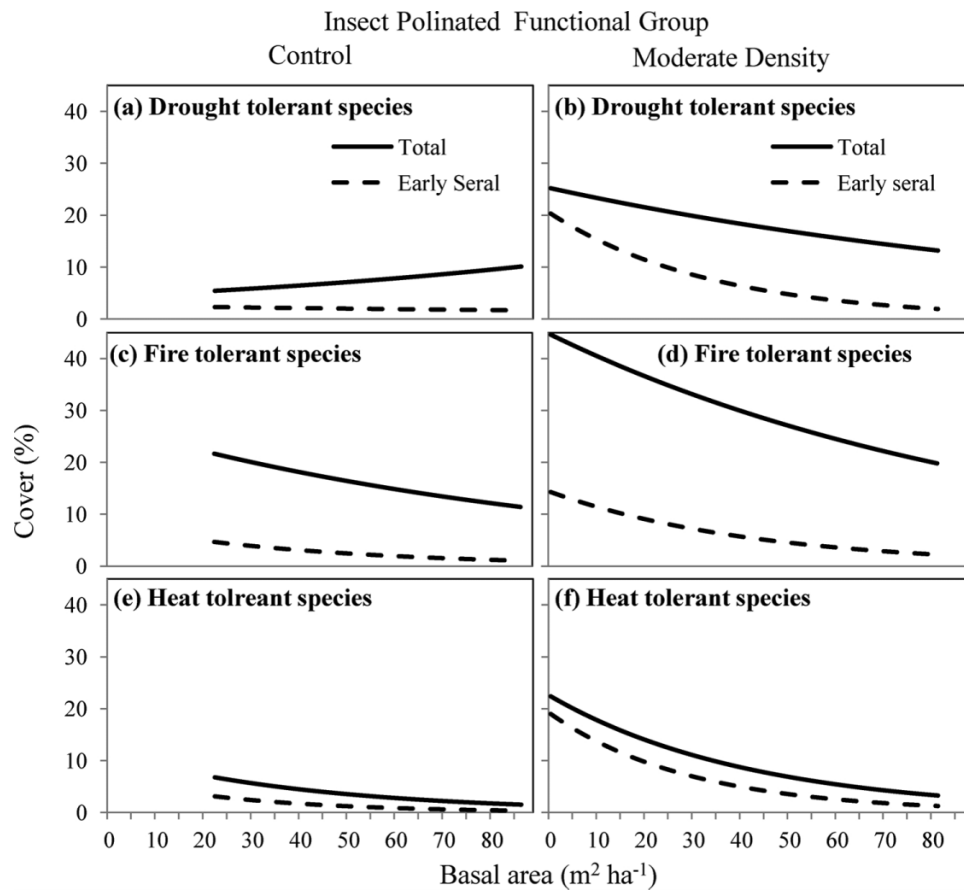
The influence of slope and aspect on radiation and other associated environmental variables has been documented (e.g., Coops et al. 2000) and is reflected in the performance of the selected functional and response-type groups. The specific impact of these variables will vary with location (e.g., the relationship between aspect and radiation varies greatly with latitudes; Coops et al. 2000), and the general management models may provide simpler predictive models, albeit at a loss of prediction accuracy (see Supplementary Table S3).

Conclusions

The conceptual model (Fig. 1) that focuses on combined effects of species traits and attributes on ecosystem functions and responses to perturbations provided insight into mechanisms and drivers impacting the adaptive capacity of ecosystems. Specifically, thinning that produced stands with lower overstory densities contributed to increased cover and diversity of wildlife forage and insect-pollinated species. As many of these species are also more tolerant to heat, drought, and disturbances, thinning leads to enhanced likelihood that the selected wildlife habitat functions are maintained under climate change conditions. This study provides an example of how information about species traits and attributes are useful for estimating impacts of forest management on ecosystem functions and adaptability. Acquiring more information about species traits and attributes will improve our ability to predict impacts of management actions and perturbations on species composition and increase our understanding of these impacts on ecosystem functions and processes. For example, the models allow assessment of which wildlife habitat functions are likely to be limited in the future and where the provision of specific functions can be improved most efficiently through thin-

nings. Alternatively, to maintain wildlife habitat quality forest management activities can limit harvesting disturbances in areas containing species with desirable traits, e.g., species more able to tolerate predicted future climate conditions, especially if they also contribute to desirable ecosystem functions and services. Predictors for such effects, however, are limited, and these relationships are likely to change along environmental gradients (Suding et al. 2008) and over time. Thus, including more detailed effects of species interactions and turnover on ecosystem functions and processes will improve the analytical approach of quantifying ecosystem adaptability.

Acknowledgements

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