AN ABSTRACT OF THE THESIS OF

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Title: <u>Overstory Density and Disturbance Impacts on the Resilience of Coniferous Forests of Western Oregon</u>.

Abstract approved:

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A trait based approach was used to assess 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, such as 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 six years following harvests. The ranges of overstory densities within thinned and unthinned stands represent gradients of resource availability and thinning disturbance. Lower overstory densities and thinnings were associated with improved ecosystem functions, specifically the provision of wildlife habitat, as evident by higher cover of flowering and fleshy-fruit and palatable leaf producing species. Greater cover of drought, fire and heat tolerant species in low density stands and after thinnings suggested that these ecosystem functions are more likely to be maintained under climate change conditions, indicating higher resilience. The response of specific functions and response types reflect the traits characteristic for each species group and the impact of these traits on sensitivity to resource availability and disturbances. Thus, the correlation between grouping criteria and the main gradients created by management activities can provide an indication of the expected vegetation response, and therefore the impact of management practices on resilience.

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Overstory Density and Disturbance Impacts on the Resilience of Coniferous Forests of Western Oregon

by Andrew R. Neill

A THESIS

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| Master of Science thesis of Andrew R. Neill presented on March 9, 2012. |
|--|
| APPROVED: |
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| I understand that my thesis will become part of the permanent collection of Oregon State libraries. My signature below authorizes the release of my thesis to any reader upon request. |
| Andrew R. Neill, Author |

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Overstory Density and Disturbance Impacts on Resilience of Coniferous Forests of Western Oregon

CHAPTER 1: INTRODUCTION TO THE STUDY

The ecological concept of resilience was introduced by C.S. Holling in 1973 (Holling 1973). Holling's initial intention was for resilience to be a descriptive term acknowledging the non-linear dynamics of ecosystem processes. The concept has since been used in social and ecological systems research to address the ability of a system to adapt to, withstand or recover from perturbations (see Brand and Jax 2007; Chapin et al. 2010; Folke et al. 2010). Later Holling (1996) distinguished two definitions he termed engineering resilience and ecological resilience. Engineering resilience is defined as the rate of return to an equilibrium or steady-state following a perturbation. The concept of engineering resilience implies the existence of equilibriums and focuses on predictability, efficiency and constancy of a system. Alternatively, ecological resilience maintains the focus on the non-linear dynamics of ecosystem processes. Ecological resilience implies that through renewal and reorganization of the primary components, such as understory species, resilient ecosystems are able to retain the same structure, identity and functions (Holling 1996; Walker et al. 2004). In contrast, resistance does not involve renewal and reorganization but maintenance of the primary components (Harrison 1979) in response to change.

Resilience *per se* is not a measurable quality of an ecosystem. The application of the resilience concept to specific parts of an ecosystem necessitates a clear identification of desired functions and perturbations (Folke et al. 2010). Resilience can therefore be referred to as specified resilience which relates to the question "resilience of what, to what?" (Carpenter et al. 2001; Folke et al. 2010). Alternatively, resilience of an ecosystem as a whole to many kinds of perturbations is termed general resilience (Folke et al. 2010).

The ability of the primary components, i.e., species, to reorganize in a way to maintain functions under altered conditions is also termed the adaptability (or adaptive

capacity) of the system which influences ecosystem resilience (Folke et al. 2010; Gunderson 2000). Disturbances play a critical role in creating structural and compositional variability across spatial and temporal scales thereby adding to adaptability and ecosystem resilience (Drever et al. 2006). Species as well as well as ecosystems have evolved and adapted to past disturbance regimes. Therefore, understating disturbance and the effects of management practices on ecosystems is essential to maintaining ecosystem functions (Bengtsson et al. 2000).

Traditional forest management practices have tended to produce more homogenous forests in terms of age, structure, composition, and function (Halpern and Spies 1995; Scheller and Mladenoff 2002; Spies and Franklin 1991). These management practices have also tended to homogenize disturbance regimes. Forest management tends to constrain the size, frequency, severity and type of disturbances that affect managed forests in order to maximize efficiency of desired ecosystem services (Drever et al. 2006; Odion and Sarr 2007; Puettmann et al. 2009). These management practices have limited the spatial and temporal variability of disturbances that promote diversity of habitats and species across a region, which theory would then predict might reduce adaptability and resilience (Buma and Wessman 2012; Pastor et al. 1998). Recently, research has explored management options that more closely represent natural disturbance regimes that act at various spatial and temporal scales with the hopes of maintaining or enhancing resilience (Bergeron et al. 1999; Drever et al. 2006; Mori 2011).

Forest ecosystems are managed to fulfill ownership objectives that often include production of multiple ecosystem goods and services such as timber harvests and wildlife habitat (Nyland 2002; Puettmann et al. 2009). Therefore, understanding impacts of management or disturbances on resilience of ecosystem goods and services to changes in timber markets or water availability may be a primary focus (Folke et al. 2002). However, when too much focus is placed on managing for specified resilience of a particular part of an ecosystem, there is risk of reducing resilience of other parts

of a system or the general resilience of the ecosystem to unexpected perturbations (Folke et al. 2010; Walker et al. 2009). Therefore, when focusing management activities on specified resilience, impacts of those activities on general resilience should be considered as well. Incorporating the resilience concept into forest management requires a change in the way society views forest ecosystems and the functions and services they provide (Folke et al. 2010; Messier and Puettmann 2011; Puettmann et al. 2009). A resilience approach requires a move away from the "command and control" strategy that focuses on optimizing productivity of a single species to one that incorporates disturbance and seeks to maintain options to adapt to altered or unforeseen changes in conditions (Drever et al. 2006).

Over the past two centuries, there has been an ongoing search for general rules that govern vegetation response to change and associations between species characteristics and biotic and abiotic factors that enable predictions of vegetation community composition and structure (Elmqvist et al. 2003; Grime 1977; Lavorel et al. 2007; Raunkiær 1934). It has been proposed that the range and strength of species traits are better at determining the effects of plants on ecosystem functioning than species diversity (Diaz and Cabido 2001). Plant traits determine a species' response to environmental conditions and mediate the effect of changes in species composition on ecosystem processes and functions (Diaz and Cabido 2001; Lavorel and Garnier 2002; Violle et al. 2007). Therefore, when examining impacts of management on ecosystem functioning it can be informative to examine combined effects of species sharing the same traits on ecosystem functions or processes (Norberg and Cumming 2008). Similarly, the overall contribution of species may be influenced by a set of traits that determine a species' response to changing environmental conditions or disturbance. Therefore, incorporation of the resilience concept into management can be done by combining functional and response traits of species into a conceptual model (Fig. 1) (Puettmann 2011). This model relates directly to the question "Resilience of what, to what?" and allows for assessment of effects of management actions or disturbance on

resilience of specific functions (Carpenter et al. 2001). "Resilience of what?" is represented by ecosystem functions and functional groups include all species with traits that affect specific ecosystem functions, e.g., the ability to fix nitrogen or produce fleshy fruits. "Resilience to what?" is represented by response types, which contain all traits that facilitate a species' ability to respond to changes in environmental conditions, e.g., deep rooting depth or waxy cuticles that lead to high drought tolerance.

Predicting ecosystem response, in terms of composition and functioning, to global change is a major challenge for ecology (Lavorel et al. 2007). The traditional focus has been based on information of historical disturbance regimes and conditions. A new method of predicting future changes is to base those predictions on relationships and patterns of current vegetation and environment. The lack of modern analogs of future climate conditions, however, makes identification of the drivers of change and their magnitude of influence difficult to assess.

In light of anticipated changes in climate, sustainable management for maintenance of ecosystem services necessitates forethought and use of management tools that enhance the ability of ecosystems to evolve and adapt to new and unexpected conditions (Puettmann et al. 2009). The impacts of climate change will directly affect vegetation through changes in resource availability and physiological processes (Chmura et al. 2011). Vegetation will also be indirectly affected through changes in species interactions within and across trophic levels and alterations to disturbance regimes. Examination of results of various management practices on distribution and abundance of species in terms of functional and response traits, as proposed above, may be more effective in achieving management goals (Lavorel et al. 2011; Puettmann 2011; Suding et al. 2008).

In this study, I use a conceptual model developed by Puettmann (2011) that considers the diversity of plant traits among species to be of greater importance than species richness for determining ecosystem functioning (Diaz and Cabido 2001;

Walker et al. 1999). I focus on the relationship between ecosystem functions and the species traits that contribute to those functions, regardless of taxonomic classification (Folke et al. 2004; Lavorel et al. 1997; Walker 1992). I work from the premise that changes in species composition that lead to changes in the abundance of species with similar traits have a direct impact on the maintenance of ecosystem functions and thus, resilience (Norberg and Cumming 2008; Petchey and Gaston 2009; Peterson et al. 1998; Walker et al. 1999). This is related to the redundancy hypothesis which proposes that a system responding to changes in conditions may leads to a reduction or elimination of species, redundant species, i.e., species that contribute to the same function, more tolerant to the altered conditions compensate for the less tolerant species (Allan et al. 2011). Previously, the concepts of functional and response type groups have been used separately to evaluate ecosystem resilience (Aubin et al. 2007; Diaz and Cabido 2001; Elmqvist et al. 2003). However, employing both concepts to evaluate ecosystem resilience, specifically maintenance of functions under changing conditions, is a critical step to better understanding the mechanisms that can affect ecosystem functioning (Hooper et al. 2005; Lavorel and Garnier 2002; Suding et al. 2008).

In summary, my research examines effects of forest management practices such as thinning on the resilience of specific ecosystem functions to specific changes in environmental conditions. I utilized data collected as part of the Density Management Study (DMS), a long term ecological research project. The overarching objective of the DMS is to examine various silvicultural methods aimed to accelerate the development of old-growth characteristics in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands of the Pacific Northwest (Cissel et al. 2006). The DMS employed variable density thinning treatments at 7 study sites across western Oregon to examine changes in overstory and understory characteristics over time. The data produced in these studies on disturbance and understory conditions created by thinning, the responses of understory species to changes in overstory density and

diversity of understory plant species and functions provide an opportunity to quantify the impacts of forest thinning on the resilience of multiple forest functions of understory vegetation. I examined how various thinning regimes influence resilience of a few specific functions by directing changes in species abundance and richness patterns. I assume that greater cover and richness of response types within functional groups indicates an increased likelihood that a system can reorganize and adapt to a wider range of surprises with little or no decrease in the provision of desired ecosystem functions (Buckland et al. 1997; Gunderson 2000; Walker et al. 1999).

LITERATURE CITED

- Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., and Hillebrand, H. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. Proceedings of the National Academy of Sciences 108(41): 17034-17039.
- Aubin, I., Gachet, S., Messier, C., and Bouchard, A. 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. Ecoscience 14(2): 259-271.
- Bengtsson, J., Nilsson, S.G., Franc, A., and Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132(1): 39-50.
- Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand-and forest-level considerations. The Forestry Chronicle 75(1): 49-54.
- Brand, F.S., and Jax, K. 2007. Focusing the meaning(s) of resilience: Resilience as a descriptive concept and a boundary object. Ecology and Society 12(1): 16.
- Buckland, S.M., Grime, J.P., Hodgson, J.G., and Thompson, K. 1997. A comparison of plant responses to the extreme drought of 1995 in northern England. Journal of Ecology 85(6): 875-882.
- Buma, B., and Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. Forest Ecology and Management 266(0): 25-33.
- Carpenter, S., Walker, B., Anderies, J.M., and Abel, N. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4(8): 765-781.

- Chapin, F., McGuire, A., Ruess, R., Hollingsworth, T., Mack, M., Johnstone, J., Kasischke, E., Euskirchen, E., Jones, J., and Jorgenson, M. 2010. Resilience of Alaska's boreal forest to climatic change. Canadian Journal of Forest Research 40(7): 1360-1370.
- Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C., and Brad St.Clair, J. 2011. Forest responses to climate change in the northwestern United States: Ecophysiological foundations for adaptive management. Forest Ecology and Management 261(7): 1121-1142.
- Cissel, J.H., Anderson, P.D., Olson, D., Puettmann, K., Berryman, S., Chan, S., and Thompson, C. 2006. BLM Density Management and Riparian Buffer Study: Establishment Report and Study Plan. U.S. Geological Survey.
- Diaz, S., and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16(11): 646-655.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., and Flannigan, M. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36(9): 2285-2299.
- Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., and Norberg, J. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1(9): 488-494.
- Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C.S., and Walker, B. 2002. Resilience and sustainable development: Building adaptive capacity in a world of transformations. Ambio 31(5): 437-440.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35: 557-581.
- Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Chapin, T., and Rockström, J. 2010. Resilience thinking: integrating resilience, adaptability and transformability. Ecology and Society 15(4): 20.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111(982): 1169-1194.
- Gunderson, L.H. 2000. Ecological resilience in theory and application. Annu. Rev. Ecol. Syst. 31: 425-439.
- Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5(4): 913-934.

- Harrison, G.W. 1979. Stability under environmental stress: Resistance, resilience, persistence, and variability. The American Naturalist 113(5): 659-669.
- Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1-23.
- Holling, C.S. 1996. Engineering resilience versus ecological resilience. In Engineering within Ecological Constraints. Edited by P. C. Schulze. National Academy Press, Washington, D. C.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75(1): 3-35.
- Lavorel, S., Díaz, S., Cornelissen, J., Garnier, E., Harrison, S., McIntyre, S., Pausas, J., Pérez-Harguindeguy, N., Roumet, C., and Urcelay, C. 2007. Plant functional types: are we getting any closer to the Holy Grail? In Terrestrial Ecosystems in a Changing World. Edited by Josep G. Canadell, Diane E. Pataki, and Louis F. Pitelka. pp. 149-164.
- Lavorel, S., and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16(5): 545-556.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J., Pellet, G., and Douzet, R. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. Journal of Ecology 99: 135-147.
- Lavorel, S., McIntyre, S., Landsberg, J., and Forbes, T.D.A. 1997. Plant functional classifications: From general groups to specific groups based on response to disturbance. Trends in Ecology & Evolution 12(12): 474-478.
- Messier, C., and Puettmann, K.J. 2011. Forests as complex adaptive systems: Implications for forest management and modelling. Italian Journal of Forest and Mountain Environments 66(3): 249-258.
- Mori, A.S. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48(2): 280-292.
- Norberg, J., and Cumming, G.S. (eds). 2008. Complexity Theory for a Sustainable Future. Columbia University Press, NY.
- Nyland, R.D. 2002. Silviculture: Concepts and Applications. 2nd ed. McGraw-Hill New York.

- Odion, D.C., and Sarr, D.A. 2007. Managing disturbance regimes to maintain biological diversity in forested ecosystems of the Pacific Northwest. Forest Ecology and Management 246(1): 57-65.
- Pastor, J., Light, S., and Sovell, L. 1998. Sustainability and resilience in boreal regions: sources and consequences of variability. Conservation Ecology [online] 2(2): 16.
- Petchey, O., and Gaston, K. 2009. Effects on ecosystem resilience of biodiversity, extinctions, and the structure of regional species pools. Theoretical Ecology 2(3): 177-187.
- Peterson, G., Allen, C.R., and Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1(1): 6-18.
- Puettmann, K.J. 2011. Silvicultural challenges and options in the context of global change: Simple fixes and opportunities for new management approaches. Journal of Forestry 109(6): 321-331.
- Puettmann, K.J., Coates, K.D., and Messier, C. 2009. A Critique of Silviculture: Managing for Complexity. Island Press, Washington, DC.
- Raunkiær, C. 1934. Life forms of plants and statistical plant geography. Arno Press.
- Scheller, R.M., and Mladenoff, D.J. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. Ecological Applications 12(5): 1329-1343.
- Spies, T.A., and Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggiero L.F., Aubry K.B., Carey A.B., Huff M.H. tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., and Navas, L. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14(5): 1125-1140.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. 2007. Let the concept of trait be functional! Oikos 116(5): 882-892.
- Walker, B., Holling, C.S., Carpenter, S.R., and Kinzig, A. 2004. Resilience, adaptability and transformability in social—ecological systems. Ecology and Society 9(2): 5. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art5.

- Walker, B., Kinzig, A., and Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2(2): 95-113.
- Walker, B.H. 1992. Biodiversity and ecological redundancy. Conservation Biology 6(1): 18-23.
- Walker, B.H., Abel, N., Anderies, J.M., and Ryan, P. 2009. Resilience, adaptability, and transformability in the Goulburn-Broken Catchment, Australia. Ecology and Society 14(1): 12.

CHAPTER 2: OVERSTORY DENSITY AND DISTURBANCE IMPACTS ON RESILIENCE OF CONIFEROUS FORESTS OF WESTERN OREGON

ABSTRACT

A trait based approach was used to assess 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, such as 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 six years following harvests. The ranges of overstory densities within thinned and unthinned stands represent gradients of resource availability and thinning disturbance. Lower overstory densities and thinnings were associated with improved ecosystem functions, specifically the provision of wildlife habitat, as evident by higher cover of flowering and fleshy-fruit and palatable leaf producing species. Greater cover of drought, fire and heat tolerant species in low density stands and after thinnings suggested that these ecosystem functions are more likely to be maintained under climate change conditions, indicating higher resilience. The response of specific functions and response types reflect the traits characteristic for each species group and the impact of these traits on sensitivity to resource availability and disturbances. Thus, the correlation between grouping criteria and the main gradients created by management activities can provide an indication of the expected vegetation response, and therefore the impact of management practices on resilience.

Introduction

Forest Resilience as an Ecological Foundation for Forest Management

Historical forest management practices that shaped managed forests have focused on increasing efficiency and reducing variability of growing and harvesting trees with the goal of achieving economic goals (Puettmann et al. 2009). Relative to historic conditions and in the absence of natural disturbance events, these practices often have led to simplified forest stand structure, composition and function (Carey et al. 1999; Franklin 1993; Halpern and Spies 1995). Partially in recognition of these effects, public sentiment shifted and management plans for many public forests now include objectives aimed at improving biological diversity and maintaining ecological functions (Bengtsson et al. 2000). Moreover, in light of increasing influences of and uncertainty associated with anthropogenic perturbations such as introduced species and climate change there is greater concern of whether recent changes in forest resource management are sufficient to maintain ecosystem goods and services (Drever et al. 2006; Puettmann 2011).

Recent efforts to study and increase the heterogeneity of forests have increased our understanding of the mechanisms which foster ecosystem resilience (Drever et al. 2006; Poage and Anderson 2007), i.e., maintain capacity for production of various ecosystem goods and services in the face of changing conditions or disturbances (Folke et al. 2002). Research examining effects of variable thinning regimes highlight impacts of forest management practices and the role of disturbance in maintaining species diversity and ecosystem goods and services of forests. With greater recognition of the contributions provided by the variety of plant species in forested ecosystems (Hagar 2007b; Vance and Thomas 1997), management objectives are increasingly incorporating understory species diversity as well as sustainability of a variety of forest goods and services, especially on public lands (Thompson et al. 2009). However, to understand whether or not management actions are influencing

ecosystem resilience it is important to determine whether or not adaptive capacity of ecosystems is gained or lost. Here adaptive capacity is defined as capacity to respond to exogenous and endogenous changes while allowing for the maintenance of ecosystem goods and services (Folke et al. 2010; Puettmann 2011).

Resilient systems contain ecological components, i.e., species, needed for adaptation to changing conditions (Walker et al. 1999). Managing to promote these ecological components should increase adaptability to novel, unexpected conditions and therefore maintain ecosystem goods and services (Folke et al. 2002; Puettmann 2011). Ecological components critical to ecosystem resilience are not necessarily organized around individual species or numbers of species, but rather the diversity of response capabilities, or plant traits, of the species that determine the system's response to change (Keddy 1992). For example, a species' contribution to an ecosystem function may decline as an adverse response of that species to an environmental perturbation. However, the ecosystem function itself may not decline if other species are less sensitive to the perturbation and contribute complementarily to the maintenance of that ecosystem function (Allan et al. 2011; Walker 1995).

Consequently, the diversity of response capabilities among species in an ecosystem is hypothesized to enhance adaptability thus maintaining functions in changing conditions and add to ecosystem resilience (Elmqvist et al. 2003; Walker 1995).

Only recently have management practices, such as thinning, on federal lands been implemented to promote and maintain heterogeneous and variable stand structure as well as economic goals (Bormann et al. 2007; Thomas et al. 2006). The goal of these forest management practices is to create variability in understory conditions more typical of unmanaged forests with the goal of improving ecosystem resilience (Thompson et al. 2009). The efficacy of recent changes in forest management practices has not been fully tested. By definition, resilient forests will be able to adapt to future environments or perturbations; e.g. warmer temperatures or insect or pathogen outbreaks, and still maintain desired functions (Folke et al. 2004). Similarly,

a resilient forest will increase opportunities to adapt management objectives and approaches to unforeseen changes; e. g., fluctuating timber markets, species invasion (Folke et al. 2002; Gunderson 2000; Olsson et al. 2004). However, few studies have directly assessed forest management impacts on resilience and adaptability of specific forest functions (Ares et al. 2010; D'Amato et al. 2011; Decocq et al. 2004; Hamilton and Haeussler 2008).

Partial removal of overstory canopy, e.g., thinning, is considered a disturbance that can create a more heterogeneous stand structure and composition (Odion and Sarr 2007; Roberts and Gilliam 1995). Forest managers and researchers are experimenting with forest thinning, gap creation and preservation of unthinned leave islands to create conditions associated with variable overstory density (Poage and Anderson 2007). Variable density thinning can create an overstory density gradient within a stand. Associated with this gradient are gradients in resource availability, microclimate, disturbance and competitive interactions between the overstory and understory plant communities (Fahey and Puettmann 2008; Hale 2003; Roberts 2004), this may strongly influence understory composition in many different forest types (see Battles et al. 2001). Increased resource availability, primarily light, to the forest understory following thinning has been linked to greater abundance of forest understory vegetation (Canham et al. 1990; Thomas et al. 1999), greater species richness (Chan et al. 2006; Reich et al. 2012; Thomas et al. 1999), and increased abundance of shade tolerant herbs (Alaback and Herman 1988; Bailey et al. 1998). In other cases, however, release of clonal shrubs following thinning can reduce species diversity through competitive exclusion (Decocq et al. 2004; Klinka et al. 1996; Thysell and Carey 2000). Along with these changes in structure and composition, thinning can increase the diversity and abundance of understory vegetation that contribute to the quality of habitat for birds (Hagar et al. 2004), mammals (Martin and McComb 2002; Suzuki et al. 2003), invertebrates (Halaj et al. 2000; Schowalter 1995; Yi and Moldenke 2005), and upland amphibians (McComb et al. 1993). Yet thinning may

lead to reduced habitat quality for species that require dense forest (Manning et al. 2012; Wessell 2005).

Disturbance related to thinning activities can also have short and long term effects on abundance and diversity of understory plant species and species trait groups (e.g., life form, seral association or shade tolerance) (Davis and Puettmann 2009; Decocq et al. 2004; Halpern and Spies 1995; Nagai and Yoshida 2006; Roberts 2004). Short-term effects can include damage to existing shrubs that provide structural and foraging habitat for understory birds (Chan et al. 2006; Hagar et al. 2004; Wilson et al. 2009). Thinning disturbance can increase light, moisture and nutrient availability and also expose soil to increase the potential for invasion by invasive exotic and native species (Davis et al. 2000; Thysell and Carey 2000), which can influence understory community dynamics (Odion and Sarr 2007, Thysell and Carey 2001). Spatial patterns of overstory retention, such as aggregate and dispersed retention and gap formation, following thinning operations can also have varying effects on understory composition and structure (Fahey and Puettmann 2007; Halpern et al. 2005; Palik et al. 2003).

A Conceptual Framework for Quantifying Forest Resilience

In light of anticipated climate change foresters must increase their understanding of whether or not effects of thinning are leading to an increase in adaptability in plant communities and therefore the resilience of ecosystem functions to warmer and drier conditions. In this study I quantify resilience within a conceptual framework adapted from Puettmann (2011) that focuses on traits and attributes that determine a species' response to changing conditions, in addition to ecosystem functions of interest (Fig. 1). This framework is based on Carpenter's (2001) metaphorical approach to resilience, "Resilience of what, to what?" To quantify resilience, specific functions of interest need to be related to specific changes in environmental conditions (Folke et al. 2010). Measurable attributes of species, such

as cover and species richness, can act as proxies for resilience if they relate a specific ecosystem function or functional group ("Resilience of what?"; top tier of Figure 1) to a specific response to a changing environmental condition or disturbance ("Resilience to what?"; second tier of Figure 1)(Suding et al. 2008). A functional group is a collection of species that perform a similar ecosystem function. The contribution of individual species to specific functions can be quantified by the species' biomass (Grime 1998). The relationship between biomass and percent cover of species can be used to estimate biomass, and therefore contribution to specific functions (Chiarucci et al. 1999; Muukkonen et al. 2006). Resilience of specific functions can be quantified if plant species within functional groups are also characterized to represent response types (McLeod and Leslie 2009). A response type is a group of species that respond similarly to a given disturbance or change in environmental conditions (Elmqvist et al. 2003). As an example, the top tier of Figure 1 has a functional group consisting of plant species that produce fleshy fruits. The species of the fleshy fruit functional group can be classified to response types (middle tier of Figure 1) based on their abilities to tolerate increases in fire frequency and intensity. By defining response types within functional groups and utilizing cover of response types as a measure of resilience, the potential sensitivity of various ecosystem functions to specific environmental changes can be examined (Grime 1998; Norberg and Cumming 2008; Puettmann 2011).

Given this framework, modifications in functional group and response type cover and richness across scales or along gradients can be evaluated to quantify changes in resilience (Allen et al. 2005). Gradients in overstory density in thinned and unthinned forests provide an opportunity to apply and evaluate this approach. By assessing changes in functional group and response type abundance under a range of overstory conditions created by thinning, the effects on resilience can be measured and information about mechanisms influencing resilience can be obtained. For example, a disturbance such as thinning may lead to increased cover of fleshy fruit producing

species and a portion of that increase is due to increased cover of fire tolerant species. Using the above framework, this would imply an increased likelihood that fleshy fruit production will be maintained under conditions of increased fire frequency and intensity.

Assessing the Utility of the Resilience Framework

The overall goal of this study is to apply the conceptual model to investigate the impacts of forest management on the resilience of forest functions related to wildlife habitat. I am using this approach to increase understanding of resilience and adaptability. Analysis of data on the sensitivity of forest understory communities of the Pacific Northwest to disturbance and environmental changes provide an good opportunity to evaluate this approach (Halpern and Spies 1995). The diversity of structure, life forms and life history strategies are indicative of the diversity of functions represented in the understory (Hagar 2007b; Halpern and Spies 1995). Managed forests provide an opportunity to look at effects of management actions on resilience and adaptability of specific ecosystem goods and services.

The primary objective of this research was to use pairings of functional groups and response types to formulate and utilize a method to quantify the resilience of specific functions to specific changes in environmental conditions. I considered three specific functional groups related to forage resources and wildlife habitat – fleshy-fruited and insect pollinated species and species whose foliage is palatable to wildlife. Species within these functional groups were further characterized as belonging to one or more of the three response types relevant to climate change – drought, fire and heat tolerant (Fig. 1).

I assessed short-term changes in understory vegetation community to gain insights into effects of overstory density and thinning on the selected functions. I further evaluated changes in abundance of species associated with these functions with respect to variations in environment as a proxy for potential changes in conditions

arising in a future climate. Four objectives are represented in the four tiers of the conceptual model (Fig.1). First, I examined the effects of overstory density and thinning on cumulative cover species that contribute to the selected functional groups as a measure of the likelihood of the provision of the selected functions (top tier of Figure 1). Second, I examined the effects of overstory density and thinning on cumulative cover of plant species that vary in drought, fire and heat tolerance. To address this objective, I examined changes in cumulative cover of response types within each functional group. Third, I investigated potential community level characteristics that may be responsible for patterns found in functional and response type group responses to overstory density presented in objectives 1 and 2. Here, I examined changes in species richness and distribution of cover among species (i.e. evenness) within response types that are responding to lower overstory densities and thereby influencing the resilience of the selected functions. Greater evenness assumes that increases in cover of functional-response type group pairings is primarily due to increased dominance of one or a few species. Lower evenness assumes a more equitable distribution of cover among species and greater contribution to cover by uncommon species. Fourth, I examined whether early seral species or selected structural components (i.e., herbs and shrubs; bottom tier of Figure 1) were influenced by overstory density and thinning, thereby driving changes in cover of response types.

METHODS

Study areas and design

This research was conducted as a component of the Density Management Study (DMS), an ongoing effort to explore options for young stand management to accelerate the development of late seral forest habitat in western Oregon while still maintaining a sustainable level of timber production (Cissel et al. 2006). The DMS has several scientific and management objectives, one of which is to evaluate the response of understory vegetation to various thinning treatments over time. The DMS includes

seven initial thinning study sites comprising 50-80 year-old planted and naturally regenerated Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands at low-elevation in the Cascade and Coast provinces of western Oregon (Table 1). The sites were selected to be representative of forested lands managed by the BLM. Although the sites were not randomly selected, they represent a wide range of elevation, soil types, and climate conditions that determine the inference scope of this study. In addition to the predominant Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) is a minor component at some sites. Hardwood species include bigleaf maple (*Acer macrophyllum* Pursh.), giant chinquapin (*Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmqvist var. *chrysophylla*), red alder (*Alnus rubra* Bong.), Pacific madrone (*Arbutus menziesii* Pursh), and Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray).

Four experimental density management treatments were imposed at each site: (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 sub-treatments of 100, 200, and 300 trees ha⁻¹ (Table 2). A portion of the area in each of the HD, MD, and VD treatment units was left unthinned in circular, 0.1, 0.2 and 0.4-ha leave island reserves and a portion of the area in the MD and VD treatment units was cut in circular, 0.1, 0.2 and 0.4-ha patch openings (Table 2). Sites were treated between 1998 and 2000. Additional site-specific stand history, site characteristics and harvest operations information are summarized in Table 1; comprehensive site and study information can be found in (Cissel et al. 2006).

Vegetation responses to the density management treatments were monitored using a nested sampling design based on permanent 0.1-ha plots. Overstory attributes were monitored using circular 0.1-ha plots (17.8 m radius) randomly positioned within each treatment. Understory vegetation was measured using four 0.002-ha circular (2.52-m radius) understory vegetation subplots per 0.1-ha overstory plot. These

subplots were established 9 m from the overstory plot center in the cardinal directions (Appendix A). A total of 77 0.1-ha plots per site were used; 14 in the CON and 21 in each of the HD, MD, and VD treatments. Each overstory plot was 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 the Bottomline site.

Plot data

Data were collected six years after thinning near peak vegetation cover (June to September). Overstory plot data included counts individual tree species ≥ 5.1 cm DBH and record of diameter at breast height (DBH). Overstory basal area (m² ha¹) was calculated from the sum of individual stem basal area (m²) of each live tree within the overstory plot. Taxonomic classifications use the USDA PLANTS Database (USDA-NRCS 2010). Topographic attributes recorded included percent slope, aspect (degree), and elevation (m). Understory subplot (0.002-ha) data included percent cover of understory vegetation by species. Understory vegetation cover was sampled by visual estimation as a percent cover of the subplot for each species not to exceed 100% for any one species. Species cover was estimated using cover classes of 1%, 5%, and 10% in 10% increments to 100%.

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 of species trait information and classifications included the USDA Plants Database (USDA-NRCS 2010) and the USDA Forest Service Fire Effects Information System (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. Species characteristics and source

information are summarized in Appendix B. When necessary trait or classification data were lacking for a species, information from similar species or varieties was considered as a potential comparison. If suitable characterizations could not be deduced, traits for a species were labeled unknown (Unk). 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 to determine the value for the characteristic of interest. For example, there are no known grasses in the PNW that produce fleshy fruit and most, if not all, grass species are wind pollinated and not insect pollinated. Classifications of response types were labeled as unknown if a species was identified only to genus. In general, a majority of the total plot cover, represented by the average of the 4 vegetation subplots, was accounted for by species that were known to have or not have the traits and attributes selected for this study. However, the presence of an individual plant or population of a species with these functional characteristics does not mean that they will produce fleshy fruit, flowers, or palatable leaves. It is assumed that greater cover of these functional groups implies greater likelihood fleshy fruits, flowers and palatable leaves will be produced (Grime 1998; Norberg and Cumming 2008).

My interpretation of resilience is based on the assumption that increased abundance of plants with specific traits or attributes implies a higher likelihood that the functions associated with those traits are maintained. The ultimate measure of the selected functions (i.e., the provision of flowers, fleshy-fruits, and palatable leaves) is the number of flowers and the biomass of fleshy-fruits and palatable leaves. Rather than developing and applying allometric equations to calculate biomass, I am using percent cover as a measure, which has been shown to be correlated to biomass (MacDonald et al. 2012; Muukkonen et al. 2006). Besides being based on the massratio hypothesis (Grime 1998), the assumption that a species' effect on a function is proportional to its cover is supported by studies that show for example that overstory removal not only increases the cover of fruiting plants but also increases the

probability that these understory plants flower and produce fruit (Harrington et al. 2002; Huffman et al. 1994; Lindh 2008; Wender et al. 2004). Similarly, palatable forage has been shown to be limiting for browse animals in dense forests and any increase would therefore result in improved wildlife habitat quality (Hagar 2007b). Early seral plants, which tend have the greatest abundance following disturbances such as thinning (Ares et al. 2009) are generally more palatable than late successional plant species(Cates and Orians 1975; Farji-Brener 2001). Also, plants are typically more palatable during early developmental stages (Fenner et al. 1999). Thus, animals are thought to benefit from greater mast and forage production following thinning in in various forest ecosystems (Bender et al. 1997; e.g., Brown 1985; Hayes et al. 2003; Muir et al. 2002).

I evaluated species response types based on traits and attributes that putatively characterize species response to a specific change in growing conditions which are predicted to be warmer and drier. However, other traits, mechanisms, and interactions with other factors may alter this response beyond what is explained by our selection of response type characteristics: drought tolerance, fire tolerance, and heat tolerance. The ultimate measure of resilience based on the selected response types would be survival and fecundity (i.e., completion of the life cycle). I examined a single year of data; however, it is likely that species with the selected response type traits would be more likely to persist in predicted future climate conditions.

To examine potential drivers of changes of cover within the response types, cumulative cover of early seral species (i.e., species that respond positively to disturbance) (Halpern 1989) and structural components (i.e., herb and shrub layer species) within response types were calculated for each plot. Species characterized as early seral associates in previous studies (Halpern and Spies 1995) and the USDA Forest Service Fire Effects Information System (USDA-Forest Service 2010) were used as representatives of early seral species. Herb layer species include forbs and grasses that are generally low-lying plant species that regenerate above ground

biomass every year and do not have persistent above ground woody stems. Conversely, the shrub layer consists of species that are generally taller understory species with prominent structural attributes, such as woody stems. 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).

Functional groups

Fleshy-fruited species

Many resident birds and mammals rely on fleshy fruits as a source of energy and migratory birds depend heavily on fruits of understory shrubs in late summer and fall (Hagar 2007a). Fleshy-fruited species include any plant species that produce 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 based on toxicity.

Insect pollinated species

Flowers contribute to the food web by attracting a variety of insects, which in turn attract a variety of insectivorous birds. This functional group includes species that are both wind and insect pollinated. A few 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 lily (*Lilium columbianum* Leichtlin) 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. All grasses were excluded from this functional group.

Palatable species

Palatability is contingent on several factors such as presence and abundance of secondary compounds, protein content, digestible energy and C:N ratio (Coley et al. 1985; Hanley et al. 2012). Palatable species are important forage for browse animals such as elk (*Cervus elaphus*) and black-tailed deer (*Odocolieus hemionus*). Information about species palatability was obtained from the USDA Plants Database (USDA-NRCS 2010) and the FEIS database (USDA-Forest Service 2010). In these databases, palatability to browse animals is rated as low, medium, and high for each species. For this study, species with either medium or high palatability ratings were classified as palatable.

Response Types

Drought tolerance

Much of the information that characterizes a species' ability to persist under dry conditions 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 example, species frequently found growing on mid- to upper-slope positions with coarse textured soils with limited moisture retention tend to be more drought tolerant than species typically found in low, moist areas with fine textured soils. For those species lacking drought tolerance characterization in the USDA Plants Database or other regional floras, I considered the typical site characteristics to assign drought tolerance (Appendix B).

Fire tolerance

Sprouting species are generally able to regenerate quickly after disturbances, such as fires. Species resprout from stem bases, rhizomes, root crowns, roots and other below ground organs that are insulated by humus or mineral soil (Rowe 1983). The capacity to resprout following death of aboveground structures was presumed indicative of a species fire tolerance. Sprouting is an important attribute of post-fire

regeneration leading to the maintenance of ecosystem functions (Bellingham and Sparrow 2000; Bond and Midgley 2001). Higher fire frequencies have been associated with a higher density of sprouting species (Bellingham and Sparrow 2000; Vlok and Yeaton 2000). Resprout capacity of shrub species is characterized 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). Since much of the species information regarding resprouting was limited to shrubs, resprouting herbs are underrepresented in this response type. Other possible mechanisms that can confer fire tolerance include avoidance by completing the life cycle prior to the typical fire season, thick bark, and persistent seeds in the seedbed that can survive the effects of fire or require fire to germinate. These traits were not easily obtainable for most species and consequently not considered in my analysis.

Heat tolerance

The average summertime (June, July and August) maximum temperature (Tmax) for the warmest county in California within the distribution of each species found on any of the DMS sites was used as a species index of heat tolerance. These indices were derived from species distributions (USDA-NRCS 2010) and long-term climate data for individual stations across California (Western Regional Climate Center 2007). Species distributions were overlain and each species ranked by Tmax which ranged from 23.7°C to 40.8°C and a median of 35.5°C. To get a coarse representation of species that are more likely to tolerate warmer temperatures, I arbitrarily split the ranking in half. The ~50% of species found within the counties with the lowest Tmax (<35.5°C) were designated as less likely to tolerate warmer temperatures than the ~50% of species found in counties with warmer average summer Tmax (>35.5°C). In addition to the assumption that Tmax is an important determinant of a species distribution, this approach also assumes that Tmax is uniform at the county level, regardless of variability in topography and local climate. Furthermore, this approach assumes genetic homogeneity where it is likely the

genotypic variation within a species varies with north-south distribution as well as distribution along an elevation gradient. I attempted to relate Tmax within a species distribution to anticipated increases in Tmax as predicted by climate models as much as 7.0°C (12.5°F) by the 2080s (Mote et al. 2008). Nearly all species could tolerate a temperature increase of that magnitude (results not shown) and the term heat tolerant thus can only be interpreted on a relative basis. More detail of species distributions, including elevation, and climate information near the bounds of a species distribution would aid in making a more accurate representation of a species tolerance to warmer temperatures.

Analytical Approach

Regression analysis was used to examine the effects of overstory density, represented by basal area, and thinning intensity or disturbance, represented by the thinning treatments, on cover, richness, and evenness of species groups. The range of overstory densities, as measured by plot basal area, within and among treatments allowed for evaluation of the influence of overstory density on understory vegetation (Fig. 2). The design of the data collection has a nested structure, i.e., subplots within plots, plots within treatment units, and treatment units within study sites. The development of explanatory models based on this hierarchical data structure warranted a mixed-model approach. Subplot values were averaged at the plot level and plot information was used in further analysis. All statistical models accounted for the nested random effects associated with study site and treatment. The global equation to describe Y_{ijk} , the mean functional group cover, mean response type cover, richness or evenness on plot k in treatment unit j on study site i is:

$$\begin{split} Y_{ijk} &= \beta_o + \beta_2 I_2 + \beta_3 I_3 + \beta_4 I_4 + \beta_5 I_5 + \beta_6 I_6 + \beta_7 x_k + \beta_8 x_k I_2 + \beta_9 x_k I_3 + \beta_{10} x_k I_4 + \\ & \beta_{11} x_k I_5 + \beta_{12} x_k I_6 + \beta_{13} slope + \beta_{14} aspect + \beta_{15} elev + \lambda_i + \gamma_{ij} + \epsilon_{ijk} \end{split}$$

where

- β_o is the fixed effect intercept coefficient of the estimate of the average plot cover in the control treatment.
- β_{2-6} are the fixed effect coefficients associated with the differences of each treatment (represented as a categorical variable) from the control as the reference.
- β_7 is the fixed effect of slope associated with basal area x of each plot k.
- β_{8-12} are the fixed effect coefficients for the slopes of the interactions between basal area and each treatment.
- β_{13} is the fixed effect associated with the percent slope of each plot k.
- β_{14} is the fixed effect associated with the aspect of each plot *k*.
- β_{15} is the fixed effect associated with the elevation of each plot *k*.
- λ_i is the random effect of the i^{th} site that adds variability to the value of Y, where i=1, 2, 3, 4, 5, 6, 7.
- γ_{ij} is the random effect of the j^{th} treatment unit on the i^{th} study site that adds variability to the value of Y, where j=1, 2, 3, 4, 5, 6.
- ε_{ijk} is the random effect of the k^{th} plot in the the j^{th} treatment unit on the i^{th} site that adds variability to the value of Y, where k=1, 2, 3, ..., 77

and $\lambda_i \sim N(0, \sigma_\lambda^2)$ and $Cov(\beta_\lambda, \beta_{\lambda'}) = 0$, $\gamma_{ij} \sim N(0, \sigma_\gamma^2)$ and $Cov(\gamma_{ij}, \gamma_{i'j'}) = 0$, $\epsilon_{ijk} \sim N(0, \sigma^2)$, and $Cov(\epsilon_{ijk}, \epsilon_{i'j'k'}) = 0$, and λ_i , γ_{ij} , ϵ_{ijk} are all independent.

Response variables include % cover, species richness and evenness of species groups. Percent species plot cover was calculated as the average percent cover across all four subplots. Species plot cover of understory vegetation within functional groups and response types was calculated as the sum of the average plot cover of all species that contribute to each group. The sum of all species cover that contributes to a group therefore can exceed 100% because of multiple vegetation layers. Hereafter cover refers to cumulative cover across species within functional groups and response types.

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 that occur on at least one of the understory subplots; therefore richness is number of species per 80 m². To quantify the differences in species dominance, Pielou's evenness index, a measure of the distribution of cover among species on a plot, was calculated from individual species cover values and species richness of each plot with the following equation:

Pielou's evenness index =
$$\frac{-\sum_{i=1}^{S} (p_i \ln p_i)}{\ln(S)}$$

where S is the total number of species on a plot and p_i is the cover of the ith species. Evenness values range from 1 to 0 with lower values indicating larger differences in cover among species. Plots with less than 2 species were omitted from this regression analysis because Pielou's evenness index cannot be calculated. The total number of plots used in regression analyses of evenness for all functional group and response type pairings are in Appendix D.8, 9 and 10.

Understory vegetation cover, richness, and evenness were evaluated as a response to a gradient in overstory density, as represented by basal area. The effects of slope (%), aspect (degree), and elevation (m) were accounted for by including these parameters in the model selection process. Aspect was transformed from the 360° compass scale to a 0-180° linear scale (linasp) for model selection and regression analyses. The conversion was completed with the following equation: linasp = 180 - |compass azimuth – 180|. This conversion gave east and west values equidistant from north the same value. Values range from 0 to 180, where 180 is south-facing and 0 is north-facing (see Warren 2008). Fit of the global model for each response variable was assessed prior to model selection and regression analyses to ensure assumptions of linear regression were met (Burnham and Anderson 2002). Where these assumptions were not met, 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. Colinearity of potential explanatory variables was

assessed using Pearson correlation coefficients. It must be noted that the figures presented herein are examples of the observed trends and only the CON and MD are represented to provide contrast between thinned and unthinned stands, although the other treatments follow similar trends. Estimates used to create the figures are presented in Appendix D and regression lines are estimated with the range of plot basal area observed in the treatments (Fig. 2). The absence of pre-treatment data makes it difficult to determine the response of individual species. Species composition prior to disturbance is a major factor determining the response and composition following disturbance (Hughes and Fahey 1991). To reduce the influence of pre-treatment conditions the analyses and conclusions concerning understory community characteristics were limited to species groups rather than individual species.

Mixed effects modeling was performed using R v 2.13.2 (R Development Core Team 2009); the function *lme()* 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 function *diversity()* from the *vegan* package.

Model selection

Assessments of thinning effects on understory vegetation were evaluated by first examining twenty-five potential models. Four hypotheses were developed to assess the importance of; a) basal area (H-1), b) treatment (H2), and c) basal area by treatment interaction (H-3) and c) to account for differences in slope, aspect and elevation (H-4). A null model (H-null) which is only a function of the random effects associated with plot, treatment unit, and site and no fixed effects was also assessed to examine the overall importance of basal area and treatment on cover, richness and evenness of the selected species groups (Appendix C). The Akaike Information Criterion (AIC_c) corrected for small sample size was used to identify models for each

hypothesis best supported by the data (Burnham and Anderson 2002). AIC_c is a parsimonious metric that rewards goodness of fit and penalizes multiple parameters. Models with the lowest AIC_c values are considered to be best supported by the data (Akaike 1973). Selection among models by AIC_c is accomplished by calculating the difference Δ_i AIC_c for each model i as:

$$\Delta_i = AIC_{ci} - AIC_{cmin}$$

where AIC_{cmin} is the lowest AIC_c value among all models fitted(Burnham and Anderson 2004). Akaike weights (w_i) were calculated as a measure of the likelihood that model i is the best model in the set as:

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$$

where R is the number of models in the set (Burnham and Anderson 2004). Akaike weights range between 0 and 1, where the values closest to 1 have the highest probability of being the best model. Inference will be derived from multiple models based on the weights and results from the fitted models that are supported by the data (Burnham and Anderson 2004).

The AIC_c analysis was used to select the appropriate error structure and the suite of models that best represents the relationship between overstory density, measured as overstory basal area (m² ha¹), and the response variables, including plant cover, species richness, and species evenness of functional and response types. The global model was used to select the appropriate structure of the nested random effects associated with plot, treatment, and site to be used in the linear mixed model approach described above. To do this, four models were evaluated: 1) only residual error associated with each plot within each treatment, 3) residual error associated with each plot within each site, and 4) a full complement error structure which included residual error associated with each plot within each plot within each treatment and site. In all but three, the random error structure best supported by the data was the full complement error structure. In the three models

where this error structure was not the best supported, the Δ_i for the full complement error structure was less than 3.00. Given the high support of this error structure in the majority of the models and the low Δ_i , this error structure was used on all models in the model selection process. Maximum likelihood was used to generate AIC_c values and restricted maximum likelihood was used when obtaining regression coefficients.

Twenty five models were examined including the null model to determine models with the best support (see Appendix C). The parameters evaluated across the set of models included 1) a categorical variable for each treatment unit (control, HD, MD, VD300, VD200, and VD100), 2) separate terms for basal area, slope (%), aspect (degree), and elevation (m), and 3) and random effect factors that were included for all models. Basal area was included as a proxy for overstory density and treatment was included as a fixed-effect, categorical variable to account for other direct and indirect effects of the thinning operation. An interaction between basal area and treatment was included to account for the potential variation in the slope of the response variable among treatments. All two-way interactions between slope, aspect, and elevation were included to account for the potential combined effects on the response variable. A three-way interaction term between slope, aspect, and elevation was not considered. Although the data for this research were collected on plots that encompass a range of slope, aspect, and elevation, the sampling design was not intended to effectively provide inference to such an interaction. However, a global model that included all parameters was considered. A good fit of a null model, which included only random effects and no fixed effects would suggest there is lack of evidence that overstory density influences the response variable and that it is a function of other parameters not included in model selection, such as the spatial relationship of plots within treatments and sites.

For several hypotheses, models with the greatest support included an interaction between treatment and basal area suggesting that the relationship between the response variable and basal area differed among one or more treatments. There

were only a limited number of plots within the VD100 treatment units, which could lead to individual plots being very influential. To evaluate the influence of the VD100 treatments, I ran an additional set of AIC_c analyses to compare support for models with the interaction term with and without inclusion of the VD100 units. If the interaction term remained in models with the highest support, it was left in the model. If the interaction term was not in the models with the highest support, the interaction term between treatment and overstory basal area was omitted from AIC_c weight calculations. Consequently, where the interaction term was excluded from model selection, inferences are limited to this reduced model set.

RESULTS

Overall understory composition varied across DMS sites. However, general trends of cover and richness of overall vegetation, functional groups and response types in relationship to overstory density were similar. More than 300 understory plant species were observed on plots across all 7 sites, with 94 to 169 species per site. Most species contributing to the selected functions had low abundance. The more abundant species in terms of mean plot cover and their associated functional and response type groups are presented in Table 3.

Impacts of thinning on cover of functional and response type groups related to wildlife habitat

Objective 1 – Influence of overstory density and thinning on overall vegetation and cover of functional 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. These relationships appeared to be consistent across variations in slope, aspect, and elevation. Understory cover of the three functional groups generally increased along natural and thinning induced gradients of decreasing overstory density. Greater cover of functional groups at lower overstory densities led to

enhanced probability of ecosystem functioning with respect to the selected functions. Models that included live tree basal area, a metric of overstory density, and thinning treatment, a categorical characterization of thinning intensity were best supported by the data as indicated by AIC_c analysis. This suggests that in addition to lower densities, factors associated with thinning, such as harvesting disturbance, are also influencing the understory vegetation community (Fig. 3). The influence of thinning intensity on understory vegetation was greater in moderately thinned stands (MD and VD) (e.g., Figs. 3a and 3b) than stands receiving the HD treatment. The response of understory vegetation to overstory density in the lowest intensity thinning (HD) generally appears to be similar to the unthinned control in the fleshy-fruited and insect pollinated functional groups. Cover of the palatable functional group was not strongly associated with treatment, indicating that palatable species cover was likely to increase with decreasing overstory density to a similar degree regardless of thinning intensities represented in this study.

Objective 2 – Influence of lower overstory density and thinning on cover of response types.

In general, cumulative cover of overall understory vegetation, the three functional groups and the nine functional group-response type pairings increased with decreasing overstory density in thinned and unthinned stands. This indicates thinning and lower overstory densities led to greater representation of selected functions by increasing the cover of drought, fire, and heat tolerant species. However, an exception to this trend was exhibited by drought-tolerant, insect-pollinated species; in unthinned stands their cover decreased from 10% to 5% of total plant cover with lower overstory densities over the basal area rage of $86 \text{ m}^2 \text{ ha}^{-1}$ to $22 \text{ m}^2 \text{ ha}^{-1}$ (Fig. 4a). This contrasts with the general trends of increasing cover with lower overstory densities and in thinned stands cover of drought-tolerant, insect-pollinated species increased from 13% to 21% for the same range of basal area. Although the trend for drought-tolerant, insect-pollinated species was represented by a model with high support (w_i =0.44), a

model that did not distinguish between unthinned and thinned stands was similarly well supported by the data (Δ_i =0.23, w_i =0.39; Appendix D.3). Cover of drought tolerant species within the fleshy-fruited and palatable functional groups appear to respond less strongly to lower overstory density compared to the overall response of understory vegetation (Figs. 5 and 6a and b).

Community characteristics and drivers impacting resilience of the selected functions

Objective 3 – Effects of lower overstory density and thinning disturbance on the species richness and evenness of response types.

Lower overstory density and thinning generally led to greater species richness of drought tolerant, fire tolerant, and heat tolerant species that contributed to the enhanced probability of production of fleshy fruit, insect pollinated flowers and palatable leaves as ecosystem functions (Figs. 4, 5 and 6c and d). For unthinned stands (therefore, in the absence of thinning disturbance) less-dense overstory was associated with greater species richness for eight of the nine functional group-response type pairings. The exception was the drought-tolerant, insect-pollinated species group. For this group, lower overstory densities in thinned stands led to greater species richness of drought tolerant insect pollinated species. In the unthinned control, however, there was no change in species richness for the same range of overstory density (Fig. 4c and 4d).

Changes in the distribution of cover among species, as measured by Pielou's evenness index were related to patterns of cover of the fire tolerant and heat tolerant functional group-response type pairings, but the trends were variable (Figs. 4, 5 and 6e and f). Overstory density or thinning did not influence evenness of drought tolerant species (see Appendix D.9-11). The patterns of evenness for heat tolerant species are likely variable because they are influenced by the low species cover (<5%) and richness (\le 4 species) in all three functional groups. This allows small changes in vegetation to have substantial impacts on evenness and brings into question the

relevance of this metric 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 within the three functional groups (e.g., Figs. 4, 5 and 6e-f). In unthinned stands, it appears that greater cover of one or a few dominant shrub species were generally responsible for the greater representation of heat tolerant species at lower overstory densities (e.g., Figs. 7c, 7f and 7i) 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. 4f, 5f and 6f). This increased the uniformity of cover among species. In the unthinned stands, lower overstory density had the opposite effect on fire-tolerant, insect-pollinated and fleshy-fruited species (Figs. 4e and 5e). In these groups dominant species had a greater response of increased growth relative to less dominant species, which is reflected in lower evenness values.

Objective 4 – Drivers responding to lower overstory density and thinning and directing changes in response type cover.

Greater cover of early seral species (e.g., *Rubus sp.* and *Holodiscus discolor* (Pursh) Maxim.) is a primary factor differentiating the response of understory cover in the thinned and unthinned stands (e.g., Figs. 8a-8f). Early seral species tended to respond positively to disturbance which indicated that disturbance associated with thinning was an important factor leading to higher resilience of the selected functions. Early seral species cover within response types was low (generally less than 2% cover) at high overstory densities (see also Appendix E). Cover of early seral species remained low at low overstory densities in unthinned stands for all nine functional group-response type pairings. In thinned stands, however, cover of early seral species within the response types was as much as 20% on plots with no overstory trees. The proportion of early seral species cover to total response type cover differed by response type. Early seral species accounted for 60% to 100% of the total plant cover of drought tolerant and heat tolerant species at low overstory density for the three

functional groups. Early seral species only accounted for ~35% of the total plant 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 the more common and dominant species, which tend to be shrubs, due to the prevalence of functional trait and response characteristics information for these species. This is particularly true for palatable and fire tolerant-palatable species. For fleshy-fruited and insect pollinated functional groups the dominant species in the shrub layer are Salal (Gaultheria shallon Pursh) and trailing blackberry (Rubus ursinus Cham. & Schltdl.). The palatable functional group was composed almost entirely of shrubs and ferns (see Figs.7g-7i). Swordfern (Polystichum munitum (Kaulf.) D. Presl), Oregon grape (Mahonia nervosa (Pursh) Nutt.) and vine maple (Acer circinatum Pursh) are dominant palatable species (Table 3). Herbs as a percentage of total cover are a minor component for each of the nine functional group-response type pairings and for the combined understory vegetation community (see Figs. 7a-7i). The insect pollinated functional group had the highest contribution to cover of the herb structural layer, although the contribution 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 (Fig. 3c and Figs. 6a and 6b). Cover values of fire tolerant and palatable species groups were not influenced by disturbance associated with the thinning treatment (w_i =0.47 and w_i =0.67 respectively; Appendices D.1 and D.7). This indicates that cover of these two groups was likely to increase with decreasing overstory density to a similar degree regardless of whether the stands had been thinned or not.

DISCUSSION

The findings presented above provide an example of the value and insights that can be gained by applying a conceptual model of ecosystem resilience as a framework to assess impacts of forest management (Fig. 1). Separating species by their traits or attributes into functional and response type groups (Lavorel et al. 1997) facilitated a quantitative assessment of thinning impacts on the resilience of specific functions provided by understory vegetation to specific perturbations (Folke et al. 2010). The analyses indicated that in the study region, lower overstory densities or management practices that effectively lowered overstory density resulted in a greater diversity of understory vegetation. Low overstory densities were associated with a higher proportion of cover and greater diversity of response types, which by definition increases ecosystem resilience. In comparison to other studies that examined harvesting effects on overall understory vegetation (for overview see Battles et al. 2001; Gilliam and Roberts 2003), functional and response type groups can respond differently to changes in resource availability and thinning disturbance. Management practices that lower overstory density will increase the likelihood of persistence by key understory species that provide nutrition for wildlife. Furthermore, the results provide insights into mechanisms and drivers affecting the enhancement of ecosystem resilience through forest management activities. While it is beyond the scope of this study to predict the impact of future climate conditions on understory species, since these effects will depend on the individualistic response of understory species to unknown future conditions (Suding et al. 2003), I hypothesize that increased species diversity within functional groups may confer greater resilience to climate change. This hypothesis could be tested in future studies.

The behavior of functional and response type groups in relation to overstory density and thinning treatments is consistent with previous work that investigated overall understory vegetation patterns (Ares et al. 2009; Davis and Puettmann 2009; Thysell and Carey 2001; Zenner et al. 2006). When compared to overall vegetation

patterns across a range of overstory conditions and thinning intensities, the response patterns of the selected functional and response type groups suggest that understanding the traits that determine a species contribution to a functional or response type group can also aid in the interpretation of potential effects of management actions on these groups. In my study, 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). Thus, relating traits characteristic of the functional groups and response types to the sensitivity of a species to resource availability and disturbances will help the understanding of the relationship between behaviors of overall understory vegetation and the selected functional groups and response types (Lavorel and Garnier 2002; Lavorel et al. 1997; Suding et al. 2008).

Influence of higher resource availability on understory vegetation

With lower overstory density, decreased resource utilization may result in increased resource availability to understory vegetation (Hale 2003; McDowell et al. 2003; Thomas et al. 1999). Whether increased availability leads to increased understory vegetation development depends on the relative availability of specific resources, such as light, water, and nutrients. For example, in wet coastal Douglas-fir and Sitka spruce (*Picea sitchensis* (Bong.) Carriere) forests of Southeast Alaska and British Columbia with abundant rainfall, increased light availability has been suggested to be the primary resource driving changes in understory vegetation (Alaback 1982; Drever and Lertzman 2003; McKenzie et al. 2000). In conditions with limited rainfall, soil moisture and nutrient levels are also important factors influencing understory plant communities (Canham et al. 1990; Harrington and Edwards 1999; Klinka et al. 1996). However, as understory light levels increase, soil moisture and nutrient availability become increasingly important in determining the response of understory vegetation (Drever and Lertzman 2001). The limited response of drought tolerant response types in all three functional groups to lower overstory densities

confirms that these species appeared to be less sensitive to low resource availability than overall vegetation (McIntyre et al. 1999; Smith and Huston 1989). Also, under higher resource availability drought tolerant species tend to be less effective at resource utilization and respond less strongly than overall vegetation (Ninemets and Valladares 2006; Sack et al. 2003).

Greater resource availability following thinning can also have negative effects on species diversity. 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). This type of response depends on site quality and is strongly dependent on pre-treatment flora (Halpern et al. 2005; Klinka et al. 1996). Competitive exclusion of other species by a dominant understory spices was not observed in my study, where recruitment of species following thinning appeared to have a homogenizing effect on species abundance within functional and response type groups (i.e., thinning produced greater evenness of abundance among species present in the understory). This is most clearly observed in results from thinned and unthinned stands for the evenness of fire tolerant species in the fleshy-fruited and insect pollinated functional groups (Figs. 4 and 5e and f). Fahey and Puettmann (2007), examining the influence of gap formation on understory vegetation at four of the DMS sites, suggested that competitive exclusion by clonal shrubs, such as salal (Gaultheria shallon Pursh) at the Bottomline site, inhibited the tendency for increased cover and recruitment of early seral and exotic species observed in gaps at other sites. The differing results between Fahey and Puettmann (2007) and those presented here are likely at least partially due to the scale of observations being examined in each study. Due to the hierarchical structure of the data, I examined effects of thinning and lower overstory density on understory vegetation across all sites. The diversity of sites, in terms of environmental conditions and species composition, provided a wide scope of inference. Evaluation of the response of vegetation within functional and

response type groups at individual sites would have been informative due to the differences in site environmental characteristics and species composition. The results of Fahey and Puettmann (2007) highlight the importance of pre-treatment flora in determining post-treatment response and suggest that species composition of functional and response type groups may vary by site which is likely to influence the response to changing overstory density. Therefore, closer examination of composition differences within functional and response type groups among study sites is an area for additional research.

Influence of thinning disturbance on understory vegetation

In contrast with indirect effects on resource availability, direct effects of thinning not associated with changes in overstory density may also influence understory vegetation. For example, residual slash or down wood can impede growth and germination of understory vegetation (Nelson and Halpern 2005). Also, thinning often influences regeneration patterns by exposing mineral soil, seed germination substrate and affecting microsite conditions (Gray and Spies 1997; Roberts 2004; Roberts and Gilliam 1995). Damage to the ground layer related to the thinning operation can increase germination substrate thereby increasing the likelihood of establishment of invasive native or introduced species (Fahey and Puettmann 2007; Roberts and Zhu 2002; Thysell and Carey 2001). However, introduced species were minor components of cover and richness of overall understory vegetation in thinned stands on DMS sites and even less so in unthinned stands (Ares et al. 2009). Obviously low cover and richness of introduced species also held for the subgroups. This is consistent with other studies in mature Douglas-fir forests where the establishment of introduced species is likely to be more limited by environmental conditions in the understory than by availability of seed (Halpern 1989; Nelson et al. 2008).

In unthinned stands, increased dominance of one or a few species, as measured by evenness, at lower overstory densities suggests that disturbance associated with the thinning treatment may play a key role in reducing the effects of competitive exclusion. The thinning operation can directly damage or kill existing vegetation and increase germination substrate and resource availability promoting the growth and recruitment of less dominant species. I observed resprouting species, mostly shrubs and ferns, dominate the selected functional and response type groups. In the absence of thinning disturbance, clonal shrubs can maintain dense patches or even continue to spread with greater resource availability at lower overstory densities in uncut forests in western Oregon, thus contributing to competitive exclusion (Fahey and Puettmann 2007; Odion and Sarr 2007; Tappeiner et al. 2001). The results from thinned and unthinned stands suggest that in the short term, thinning not only led to greater resilience through greater cover and species richness within response types. However, observations in gaps at the Bottomline site by Fahey and Puettmann (2007) suggested that even the high levels of disturbance associated with gap formation may not be enough to interrupt the competitive effects of dominant species.

Harvesting activities have a direct impact on the understory by damaging or killing understory vegetation. In a similar study in Douglas-fir stands of the Oregon Coast Range, damage to understory vegetation due to the harvesting operation initially reduced shrub cover. Shrub cover recovered to pre-treatment conditions within 5 years (Chan et al. 2006). In similar studies in the Oregon Cascades, short shrubs recovered from initial damage within 5-7 years following thinning (Davis and Puettmann 2009), but tall shrubs took 10 years or longer to recover to levels in unthinned stands (Wilson and Puettmann 2007). For the functions considered in this study (e.g., flower, fleshy-fruit and palatable leaf producing species), the predominant species were mostly shrub layer species. Therefore, direct impacts of the 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.

Sprouting species damaged by the harvesting operation will recover at various rates and increase contribution to the selected functions until increased competition for resources from overstory trees begins to inhibit growth. It is likely that as effects of thinning disturbance decrease the influence of the overstory will increasingly shape patterns of understory vegetation by decreasing resource availability through increased competition by overstory trees (Lindh and Muir 2004).

Fire tolerant species were selected based on their ability to resprout after fires or other disturbances (Bellingham and Sparrow 2000; Bond and Midgley 2001; Weiher et al. 1999), which in my study biased selection towards perennial shrubs and ferns, since information about fire tolerance (i.e. resprouting ability) was mostly limited to shrubs and ferns. As discussed above, it is likely that shrubs and ferns are still recovering from direct damage from the harvesting operation in thinned stands, making the interpretation of the response of fire tolerant response types speculative. Published evidence of fire tolerance was mostly lacking for forbs and grasses. Consequently, these species were not included in the fire tolerant response type and their influence is likely underrepresented. Had information regarding fire tolerance of forbs and grasses been available, the trends may have been more similar to overall vegetation patterns since these species would likely have been faster to recover.

Combined influence of resource availability and thinning disturbance on understory vegetation

A greater cover and richness of early seral species in thinned stands was the primary driver of treatment differences in the relationship between basal area and cover and richness of the functional groups and functional group-response type pairings. Early seral species such as trailing blackberry (*Rubus ursinus* Cham. & Schltdl.), common whipplea (*Whipplea modesta* Torr.) and oceanspray (*Holodiscus discolor* (Pursh) Maxim.) respond positively to resources made available following disturbance and typically have the greatest abundance following disturbance (Halpern 1989; Halpern and Spies 1995; Odion and Sarr 2007). Using the same data, Ares et al. (2009) observed greater overall cover and richness of early seral shrubs and forbs in thinned stands compared to unthinned controls. The response of early seral vegetation

may also explain the behavior of the heat tolerant response type. Heat tolerant species in my sample are also early seral (Pearson correlation coefficient=0.98). More open conditions, such as those created by thinning, result in higher variability in ambient air and soil temperatures extremes (Heithecker and Halpern 2006) thus benefiting species that can tolerate these extremes.

Influence of various thinning intensities on understory vegetation

A lack of response to low levels of thinning (HD) suggests that moderate to heavy levels of thinning (MD and VD) may be required to generate increased cover of the insect pollinated and fleshy-fruited functional groups and their response types (Fig. 3a and 3b). 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 post-harvest. Thinning intensities greater than observed in the HD are more likely to increase the abundance and diversity of understory species for prolonged periods of time. However other studies, including some of which used the same sites, 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); vegetation patterns were observed to be similar among treatments although differences between thinned and unthinned stands were detected.

Scale of observations and the degree of overlap of sampled overstory densities in the CON and HD treatment versus the other treatments (Fig. 2) may explain some of the inconsistencies of vegetation response to thinning among studies. In contrast to studies that compared treatment averages and showed no differences of cover and richness among treatments (e.g., Ares et al. 2009; Davis and Puettmann 2009), I analyzed the vegetation response at a small scale plot level (80 m² ha⁻¹). Variability in pre-harvest stand density and irregular thinning intensities due to operational constraints or the presence of patch openings and leave islands can increase the within treatment plot-to-plot variability of species cover and richness (Halpern et al. 2005).

CONCLUSIONS

The use of a conceptual model (see Fig. 1) that focuses on the combined effects of species traits and attributes on ecosystem functions and response to perturbations following thinning provided insights into the mechanisms and drivers that are impacting resilience of ecosystems. Specifically, forest thinning that produced stands with lower overstory densities contributed to increased cover and diversity of wildlife forage species. When these species are also more tolerant to changes in climate conditions, thinning leads to enhanced resilience with respect to specific functions under climate change. This study provides an example how information about species traits are useful for estimating impacts of forest management on ecosystem functions and resilience. Acquiring more information on species traits and attributes will improve our ability to predict the impacts of management actions and perturbations on patterns of species composition and our understanding of how management actions and perturbations may alter ecosystem functions and processes. For example, in order to maintain wildlife habitat quality, forest management activities can focus on harvesting or thinning in areas that avoid damaging desired or sensitive species or can increase thinning disturbance levels in areas dominated by species with potential for competitive exclusion of other species. Likewise, in light of future climate change, species more able to tolerate predicted conditions could be targeted for protection, enhancement and recruitment to increase the abilities of these species to contribute to selected functions under changing conditions. This approach of quantifying resilience can be improved by including the effects of species interactions and turnover on ecosystem functions and processes. Predictors for such effects, however, are limited and are likely to change along environmental gradients (Suding et al. 2008).

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LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 in International symposium on information theory. Springer Verlag, Akademiai Kiado, Budapest.
- Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63:1932-1948.
- Alaback, P. B. and F. Herman. 1988. Long-term response of understory vegetation to stand density in Picea-Tsuga forests. Canadian Journal of Forest Research 18:1522-1530.
- Allan, E., W. Weisser, A. Weigelt, C. Roscher, M. Fischer, and H. Hillebrand. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. Proceedings of the National Academy of Sciences 108:17034-17039.
- Allen, C., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8:958-966.
- Ares, A., S. D. Berryman, and K. J. Puettmann. 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. Applied Vegetation Science 12:472-487.
- Ares, A., A. R. Neill, and K. J. Puettmann. 2010. Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. Forest Ecology and Management 260:1104-1113.

- Bailey, J. D., C. Mayrsohn, P. S. Doescher, E. St Pierre, and J. C. Tappeiner. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. Forest Ecology and Management 112:289-302.
- Battles, J. J., A. J. Shlisky, R. H. Barrett, R. C. Heald, and B. H. Allen-Diaz. 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. Forest Ecology and Management 146:211-222.
- Bellingham, P. J. and A. D. Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89:409-416.
- Bender, L. C., D. L. Minnis, and J. B. Haufler. 1997. Wildlife responses to thinning red pine. Northern Journal of Applied Forestry 14:141-146.
- Bengtsson, J., S. G. Nilsson, A. Franc, and P. Menozzi. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132:39-50.
- Bond, W. J. and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution 16:45-51.
- Bormann, B. T., R. W. Haynes, and J. R. Martin. 2007. Adaptive management of forest ecosystems: Did some rubber hit the road? Bioscience 57:186-191.
- Brown, E. R. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. US Department of Agriculture, Forest Service, Pacific Northwest Region.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.
- Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference. Sociological Methods & Research 33:261.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620-631.
- Carey, A. B., C. C. Maguire, B. L. Biswell, and T. M. Wilson. 1999. Distribution and abundance of Neotoma in western Oregon and Washington. Northwest Science 73:65-80.
- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4:765-781.
- Cates, R. G. and G. Orians, H. . 1975. Sucessional status and the palatability of plants to generalized herbivores. Ecology 56:410-418.

- Chan, S. S., D. J. Larson, K. G. Maas-Hebner, W. H. Emmingham, S. R. Johnston, and D. A. Mikowski. 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. Canadian Journal of Forest Research 36:2696-2711.
- Chiarucci, A., J. B. Wilson, B. J. Anderson, and V. De Dominicis. 1999. Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? Journal of Vegetation Science 10:35-42.
- Cissel, J. H., P. D. Anderson, D. Olson, K. Puettmann, S. Berryman, S. Chan, and C. Thompson. 2006. BLM Density Management and Riparian Buffer Study: Establishment Report and Study Plan. U.S. Geological Survey.
- Coley, P., J. Bryant, and F. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science 230:895.
- D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. Forest Ecology and Management 262:803-816.
- Davis, L. R. and K. J. Puettmann. 2009. Initial response of understory vegetation to three alternative thinning treatments. Journal of Sustainable Forestry 28:904-934.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology 88:528-534.
- Decocq, G., M. Aubert, F. Dupont, D. Alard, R. Saguez, A. Wattez-Franger, B. De Foucault, A. Delelis-Dusollier, and J. Bardat. 2004. Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. Journal of Applied Ecology 41:1065-1079.
- Drever, C. R. and K. P. Lertzman. 2001. Light-growth responses of coastal Douglasfir and western redcedar saplings under different regimes of soil moisture and nutrients. Canadian Journal of Forest Research 31:2124-2133.
- Drever, C. R. and K. P. Lertzman. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research 33:137-146.
- Drever, C. R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36:2285-2299.
- Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488-494.

- Fahey, R. T. and K. J. Puettmann. 2007. Ground layer disturbance and initial conditions influence gap partitioning of understorey vegetation. Journal of Ecology 95:1098-1109.
- Fahey, R. T. and K. J. Puettmann. 2008. Patterns in spatial extent of gap influence on understory plant communities. Forest Ecology and Management 255:2801-2810.
- Farji-Brener, A. G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. Oikos 92:169-177.
- Fenner, M., M. E. Hanley, and R. Lawrence. 1999. Comparison of seedling and adult palatability in annual and perennial plants. Functional Ecology 13:546-551.
- Folke, C., S. Carpenter, T. Elmqvist, L. Gunderson, C. S. Holling, and B. Walker. 2002. Resilience and sustainable development: Building adaptive capacity in a world of transformations. Ambio 31:437-440.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics 35:557-581.
- Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Chapin, and J. Rockström. 2010. Resilience thinking: integrating resilience, adaptability and transformability. Ecology and Society 15:20.
- Franklin, J. F. 1993. Lessons from old-growth: Fueling controversy and providing direction. Journal of Forestry 91:10-13.
- Gilkey, H. M. and L. J. Dennis. 2001. Handbook of Northwestern plants. Oregon State University Press, Corvallis, OR.
- Gilliam, F. S. and M. R. Roberts. 2003. The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, USA.
- Gray, A. N. and T. A. Spies. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78:2458-2473.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344-347.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902-910.
- Gunderson, L. H. 2000. Ecological resilience in theory and application. Annual Review of Ecology and Systematics 31:425-439.

- Hagar, J., S. Howlin, and L. Ganio. 2004. Short-term response of songbirds to experimental thinning of young Douglas-fir forests in the Oregon Cascades. Forest Ecology and Management 199:333-347.
- Hagar, J. C. 2007a. Key elements of stand structure for wildlife in production forests west of the Cascade Mountains. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-695, Portland, OR.
- Hagar, J. C. 2007b. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. Forest Ecology and Management 246:108-122.
- Halaj, J., D. W. Ross, and A. R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90:139-152.
- Hale, S. E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. Forest Ecology and Management 179:341-349.
- Halpern, C. B. 1989. Early successional patterns of forest species interactions of life-history traits and disturbance. Ecology 70:704-720.
- Halpern, C. B., D. McKenzie, S. A. Evans, and D. A. Maguire. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecological Applications 15:175-195.
- Halpern, C. B. and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5:913-934.
- Hamilton, E. H. and S. Haeussler. 2008. Modeling stability and resilience after slashburning across a sub-boreal to subalpine forest gradient in British Columbia. Canadian Journal of Forest Research 38:304-316.
- Hanley, T. A., D. E. Spalinger, K. J. Mock, O. L. Weaver, and G. M. Harris. 2012. Forage resource evaluation system for habitat—deer: an interactive deer habitat model. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-858.
- Harrington, C. A., K. R. Buermeyer, L. C. Brodie, and B. W. Wender. 2002. Factors influencing growth and flowering of understory plants in conifer stands in western Washington. Page 159. US Dept. of Agriculture, Forest Service, Pacific Northwest Research Station.
- Harrington, T. B. and M. B. Edwards. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. Canadian Journal of Forest Research 29:1055-1064.

- Hayes, J. P., J. M. Weikel, and M. M. P. Huso. 2003. Response of birds to thinning young Douglas-fir forests. Ecological Applications 13:1222-1232.
- Heithecker, T. D. and C. B. Halpern. 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management 226:60-71.
- Hitchcock, C. L. and A. Cronquist. 2001. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.
- Huffman, D. W., J. C. Tappeiner II, and J. C. Zasada. 1994. Regeneration of salal (Gaultheria shallon) in the central Coast Range forests of Oregon. Canadian Journal of Botany 72:39-51.
- Hughes, J. W. and T. J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. Journal of Ecology 79:605-616.
- Jordano, P. 2000. Fruits and frugivory. Pages 125-166 in M. Fenner, editor. Seeds: The Ecology of Regeneration in Plant Communities. CABI Publ., Wallingford, UK.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157-164.
- Klinka, K., H. Y. H. Chen, Q. Wang, and L. De Montigny. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on west Vancouver Island. Northwest Science 70:193-200.
- Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545-556.
- Lavorel, S., S. McIntyre, J. Landsberg, and T. D. A. Forbes. 1997. Plant functional classifications: From general groups to specific groups based on response to disturbance. Trends in Ecology & Evolution 12:474-478.
- Lindh, B. and P. Muir. 2004. Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? Forest Ecology and Management 192:285-296.
- Lindh, B. C. 2008. Flowering of understory herbs following thinning in the western Cascades, Oregon. Forest Ecology and Management 256:929-936.
- MacDonald, R. L., J. M. Burke, H. Y. H. Chen, and E. E. Prepas. 2012. Relationship between aboveground biomass and percent cover of ground vegetation in Canadian Boreal Plain riparian forests. Forest Science 58:47-53.

- Manning, T., J. C. Hagar, and B. C. McComb. 2012. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. Forest Ecology and Management 264:115-124.
- Martin, K. J. and W. C. McComb. 2002. Small mammal habitat associations at patch and landscape scales in Oregon. Forest Science 48:255-264.
- McComb, W. C., K. McGarigal, and R. G. Anthony. 1993. Small mammal and amphibian abundace in streamside and upslope habits of mature Douglas-fir stands. Northwest Science 67:7-15.
- McDowell, N., J. Brooks, S. Fitzgerald, and B. Bond. 2003. Carbon isotope discrimination and growth response of old Pinus ponderosa trees to stand density reductions. Plant, Cell & Environment 26:631-644.
- McIntyre, S., S. Díaz, S. Lavorel, and W. Cramer. 1999. Plant functional types and disturbance dynamics Introduction. Journal of Vegetation Science 10:603-608.
- McKenzie, D., C. B. Halpern, and C. R. Nelson. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, USA. Canadian Journal of Forest Research 30:1655-1666.
- McLeod, K. and H. Leslie. 2009. Ecosystem-Based Management for the Oceans. Cambridge Univ Press.
- Mote, P., E. Salathé, V. Duilére, and E. Jump. 2008. Scenarios of Future Climate for the Pacific Northwest. University of Washington, Seattle, WA.
- Muir, P. S., R. L. Mattingly, J. C. Tappeiner, J. D. Bailey, W. E. Elliott, J. C. Hagar, J. C. Miller, E. B. Peterson, and E. E. Starkey. 2002. Managing for biodiversity in young Douglas-fir forests of western Oregon. US Geological Survey, Forest and Rangeland Ecosystem Science Center.
- Muukkonen, P., R. Makipaa, R. Laiho, K. Minkkinen, H. Vasander, and L. Finér. 2006. Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. Silva Fennica 40:231.
- Nagai, M. and T. Yoshida. 2006. Variation in understory structure and plant species diversity influenced by silvicultural treatments among 21-to 26-year-old Picea glehnii plantations. Journal of Forest Research 11:1-10.
- Natureserve. 2010. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.0. NatureServe, Arlington, VA. U.S.A. Available http://www.natureserve.org/explorer. (Accessed: October 2010)
- Nelson, C. R. and C. B. Halpern. 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Canadian Journal of Botany 83:610-620.

- Nelson, C. R., C. B. Halpern, and J. K. Agee. 2008. Thinning and burning result in low-level invasion by nonnative plants but neutral effects on natives. Ecol Appl 18:762-770.
- Ninemets, Ü. and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76:521-547.
- Norberg, J. and G. S. Cumming, editors. 2008. Complexity Theory for a Sustainable Future. Columbia University Press, NY.
- Odion, D. C. and D. A. Sarr. 2007. Managing disturbance regimes to maintain biological diversity in forested ecosystems of the Pacific Northwest. Forest Ecology and Management 246:57-65.
- Olsson, P., C. Folke, and F. Berkes. 2004. Adaptive comanagement for building resilience in social-ecological systems. Environmental Management 34:75-90.
- Palik, B., R. J. Mitchell, S. Pecot, M. Battaglia, and M. Pu. 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. Ecological Applications 13:674-686.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. D. C. Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models.
- Poage, N. J. and P. D. Anderson. 2007. Large-scale silviculture experiments fo western Oregon and Washington. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-713, Portland, OR.
- Pojar, J. and A. Mackinnon. 1994. Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia, and Alaska. Lone Pine Publishing, Redmond, OR.
- Puettmann, K. J. 2011. Silvicultural challenges and options in the context of global change: Simple fixes and opportunities for new management approaches. Journal of Forestry 109:321-331.
- Puettmann, K. J., K. D. Coates, and C. Messier. 2009. A Critique of Silviculture: Managing for Complexity. Island Press, Washington, DC.
- R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P. B., L. E. Frelich, R. A. Voldseth, P. Bakken, and C. Adair. 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. Journal of Ecology:no-no.

- Roberts, M. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Botany 82:1273-1283.
- Roberts, M. and L. Zhu. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. Forest Ecology and Management 155:17-31.
- Roberts, M. R. and F. S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. Ecological Applications 5:969-977.
- Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. Pages 135-154 in W. R. W. and M. D. A., editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons Ltd.
- Sack, L., P. J. Grubb, and T. Marañón. 2003. The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. Plant Ecology 168:139-163.
- Schowalter, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. Forest Ecology and Management 78:115-125.
- Smith, T. and M. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. Plant Ecology 83:49-69.
- Stewart, R. E. 1975. Allelopathic potential of western bracken. Journal of Chemical Ecology 1:161-169.
- Suding, K. N., D. E. Goldberg, and K. M. Hartman. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84:1-16.
- Suding, K. N., S. Lavorel, F. S. Chapin III, J. H. C. Cornelissen, S. Diaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and L. Navas. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14:1125-1140.
- Suzuki, Nobuya, Hayes, and P. John. 2003. Effects of thinning on small mammals in Oregon Coastal Forests. The Journal of Wildlife Management 67:352-371.
- Tappeiner, J. C., J. C. Zasada, D. W. Huffman, and L. M. Ganio. 2001. Salmonberry and salal annual aerial stem production: the maintenance of shrub cover in forest stands. Canadian Journal of Forest Research 31:1629-1638.
- The_Calflora_Database. 2010. Calflora: Information on California plants for education, research and conservation. [web application]. 2008. Berkeley, California: The Calflora Database [a non-profit organization]. Available: http://www.calflora.org/ (Accessed: Oct 11, 2010).

- Thomas, J. W., J. F. Franklin, J. Gordon, and K. N. Johnson. 2006. The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. Conservation Biology 20:277-287.
- Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: Understory responses to thinning and fertilization. Ecological Applications 9:864-879.
- Thompson, I., B. Mackey, S. McNulty, and A. Mosseler. 2009. Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecoystems., Secretariat of the Convention on Biological Diversity. CBD Technical Series no. 43, Montreal, Canada.
- Thysell, D. and A. Carey. 2000. Effects of forest management on understory and overstory vegetation: A retrospective study. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-488, Portland, OR.
- Thysell, D. R. and A. B. Carey. 2001. Manipulation of density of Pseudotsuga menziesii canopies: preliminary effects on understory vegetation. Canadian Journal of Forest Research 31:1513-1525.
- USDA-Forest Service. 2010. Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis [2010, October 11].
- USDA-NRCS. 2010. The PLANTS Database (http://plants.usda.gov, 27 August 2010). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- Vance, N. C. and J. Thomas, editors. 1997. Special forest products: biodiversity meets the marketplace. U.S. Department of Agriculture, Forest Service, General Technical Report WO-GTR-063, Washington, DC.
- Vlok, J. and R. Yeaton. 2000. The effect of short fire cycles on the cover and density of understorey sprouting species in South African mountain fynbos. Diversity and Distributions 6:233-242.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology 9:747-752.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2:95-113.

- Warren, R. J. 2008. Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position. Plant Ecology 198:297-308.
- Weiher, E., W. Adrie, T. Ken, R. Michael, G. Eric, and E. Ove. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science 10:609-620.
- Wender, B. W., Harrington, C. A., Tappeiner, and J. C. 2004. Flower and fruit production of understory shrubs in western Washington and Oregon. Northwest Science 78:17.
- Wessell, S. J. 2005. Biodiversity in managed forests of western Oregon: Species assemblages in leave islands, thinned, and unthinned forests. Oregon State University, Corvallis, OR.
- Western Regional Climate Center. 2007. California climate summaries. Reno, NV.
- Wilson, D. S., P. D. Anderson, and K. J. Puettmann. 2009. Evaluating the consistency of understorey vegetation response to forest thinning through synthetic analysis of operational-scale experiments. Forestry 82:583-596.
- Wilson, D. S. and K. J. Puettmann. 2007. Density management and biodiversity in young Douglas-fir forests: Challenges of managing across scales. Forest Ecology and Management 246:123-134.
- Yi, H. and A. Moldenke. 2005. Response of ground-dwelling arthropods to different thinning intensities in young Douglas-fir forests of western Oregon. Environmental entomology 34:1071-1080.
- Zenner, E. K., J. M. Kabrick, R. G. Jensen, J. E. Peck, and J. K. Grabner. 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. Forest Ecology and Management 222:326-334.

CHAPTER 3: SYNTHESIS

The approach used in this research allowed for the quantification of the impacts of forest management on ecosystem resilience. Although I examined specific functions and response types, this approach can easily be adapted to incorporate other functions and potential perturbations (Puettmann 2011). This approach can be tailored to meet specific management objectives that aim to improve the ecosystem resilience. The combination of functional and response traits and attributes in this model adds to the body of research aiming to predict ecosystem response in terms of species composition and effects on ecosystem functioning (Diaz et al. 2004; Elmqvist et al. 2003; Hooper et al. 2005; Suding et al. 2008).

The trait and attribute information available in the literature was biased toward common species. This may have led to underestimation of the combined contribution of less common species to functional and response type groups. However, the importance of the contributions of less dominant species may be better measured as their contribution to ecosystem resilience in terms of their capacity to adapt to altered climate conditions (Allan et al. 2011; Suding et al. 2008; Walker et al. 1999). As trait information is improved and expanded to include less dominant species, the accuracy of trait based research will also be improved (Garnier et al. 2007). Recent efforts to create regional and global plant trait databases that compile standardized trait based information are promising (see Kattge et al. 2011). Relevant species trait information being collected includes traits that determine a species response to environmental factors and that affect ecosystem processes and functions.

In the research presented here, species were characterized as drought tolerant and temperature tolerant. These are "yes" or "no" attributes that are likely the outcome of several plant traits that allow a species to tolerate warmer or drier conditions. In this sense, a comprehensive traits database could provide a measureable quality of a species, such as rooting depth or leaf thickness that could then be used to

quantify a species relative tolerance as opposed to the absolute measures I have used here.

I assumed that a species contribution to functional and response type groups was proportional to its abundance. However, it is not likely that species contribute equally. The level of contribution may vary along environmental gradients and depend on competitive interactions (Suding et al. 2008). Furthermore, I assessed traits and attributes that relate to species response capabilities to specific changes in conditions. However, the effects of compounded disturbances are likely to have differing effects on species composition which will influence ecosystem processes (Buma and Wessman 2012). These are factors not easily accounted for and are topics of further research. My research could be improved by examining changes in the relative contribution of individual species to get a better idea of the effects of dominant species on ecosystem functions but lack of pretreatment data makes this difficult.

My research presents evidence that lower overstory densities and thinning enhanced the resilience of understory vegetation components related to wildlife habitat in managed Douglas-fir forests of the Pacific Northwest. This is one of the main objectives of the DMS (Cissel et al. 2006). Although the stands on the DMS sites were thinned to target tree densities, the residual overstory densities within thinned and unthinned stands were variable. This resulted in significant overlap of overstory densities among treatment areas. Therefore, plot level regression analyses could be conducted to examine understory vegetation response across a range of overstory conditions. The observation of a non-linear response of understory vegetation to overstory thinning indicates that thinning intensities observed in the MD and VD treatments are more likely to achieve long lasting effects on the understory vegetation, in terms of species abundance and diversity within the functional and response type groups.

LITERATURE CITED

- Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., and Hillebrand, H. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. Proceedings of the National Academy of Sciences 108(41): 17034-17039.
- Buma, B., and Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. Forest Ecology and Management 266(0): 25-33.
- Cissel, J.H., Anderson, P.D., Olson, D., Puettmann, K., Berryman, S., Chan, S., and Thompson, C. 2006. BLM Density Management and Riparian Buffer Study: Establishment Report and Study Plan. U.S. Geological Survey.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg. Sci. 15(3): 295-304.
- Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., and Norberg, J. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1(9): 488-494.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., and Golodets, C. 2007. Assessing the effects of landuse change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. Annals of Botany 99(5): 967.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75(1): 3-35.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bonisch, G., Garnier, E., Westboy, M., Reich, P.B., and Wright, I.A. 2011. TRY—a global database of plant traits. Global Change Biology 17(9): 2905-2935.

- Puettmann, K.J. 2011. Silvicultural challenges and options in the context of global change: Simple fixes and opportunities for new management approaches. Journal of Forestry 109(6): 321-331.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., and Navas, L. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14(5): 1125-1140.
- Walker, B., Kinzig, A., and Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2(2): 95-113.

BIBLIOGRAPHY

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In International symposium on information theory. Edited by Petrov B.N., and Csaki F. Springer Verlag, Akademiai Kiado, Budapest. pp. 267-281.
- Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63(6): 1932-1948.
- Alaback, P.B., and Herman, F. 1988. Long-term response of understory vegetation to stand density in Picea-Tsuga forests. Canadian Journal of Forest Research 18(12): 1522-1530.
- Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., and Hillebrand, H. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. Proceedings of the National Academy of Sciences 108(41): 17034-17039.
- Allen, C., Gunderson, L., and Johnson, A.R. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8(8): 958-966.
- Ares, A., Berryman, S.D., and Puettmann, K.J. 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. Applied Vegetation Science 12(4): 472-487.
- Ares, A., Neill, A.R., and Puettmann, K.J. 2010. Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. Forest Ecology and Management 260(6): 1104-1113.
- Aubin, I., Gachet, S., Messier, C., and Bouchard, A. 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. Ecoscience 14(2): 259-271.
- Bailey, J.D., Mayrsohn, C., Doescher, P.S., St Pierre, E., and Tappeiner, J.C. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. Forest Ecology and Management 112(3): 289-302.
- Battles, J.J., Shlisky, A.J., Barrett, R.H., Heald, R.C., and Allen-Diaz, B.H. 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. Forest Ecology and Management 146(1-3): 211-222.
- Bellingham, P.J., and Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89(2): 409-416.
- Bender, L.C., Minnis, D.L., and Haufler, J.B. 1997. Wildlife responses to thinning red pine. Northern Journal of Applied Forestry 14(3): 141-146.

- Bengtsson, J., Nilsson, S.G., Franc, A., and Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132(1): 39-50.
- Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand-and forest-level considerations. The Forestry Chronicle 75(1): 49-54.
- Bond, W.J., and Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution 16(1): 45-51.
- Bormann, B.T., Haynes, R.W., and Martin, J.R. 2007. Adaptive management of forest ecosystems: Did some rubber hit the road? Bioscience 57(2): 186-191.
- Brand, F.S., and Jax, K. 2007. Focusing the meaning(s) of resilience: Resilience as a descriptive concept and a boundary object. Ecology and Society 12(1): 16.
- Brown, E.R. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. US Department of Agriculture, Forest Service, Pacific Northwest Region.
- Buckland, S.M., Grime, J.P., Hodgson, J.G., and Thompson, K. 1997. A comparison of plant responses to the extreme drought of 1995 in northern England. Journal of Ecology 85(6): 875-882.
- Buma, B., and Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. Forest Ecology and Management 266(0): 25-33.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Burnham, K.P., and Anderson, D.R. 2004. Multimodel inference. Sociological Methods & Research 33(2): 261.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20(5): 620-631.
- Carey, A.B., Maguire, C.C., Biswell, B.L., and Wilson, T.M. 1999. Distribution and abundance of Neotoma in western Oregon and Washington. Northwest Science 73(2): 65-80.
- Carpenter, S., Walker, B., Anderies, J.M., and Abel, N. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4(8): 765-781.
- Cates, R.G., and Orians, G., H. . 1975. Successional status and the palatability of plants to generalized herbivores. Ecology 56(2): 410-418.

- Chan, S.S., Larson, D.J., Maas-Hebner, K.G., Emmingham, W.H., Johnston, S.R., and Mikowski, D.A. 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. Canadian Journal of Forest Research 36(10): 2696-2711.
- Chapin, F., McGuire, A., Ruess, R., Hollingsworth, T., Mack, M., Johnstone, J., Kasischke, E., Euskirchen, E., Jones, J., and Jorgenson, M. 2010. Resilience of Alaska's boreal forest to climatic change. Canadian Journal of Forest Research 40(7): 1360-1370.
- Chiarucci, A., Wilson, J.B., Anderson, B.J., and De Dominicis, V. 1999. Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? J. Veg. Sci. 10(1): 35-42.
- Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C., and Brad St.Clair, J. 2011. Forest responses to climate change in the northwestern United States: Ecophysiological foundations for adaptive management. Forest Ecology and Management 261(7): 1121-1142.
- Cissel, J.H., Anderson, P.D., Olson, D., Puettmann, K., Berryman, S., Chan, S., and Thompson, C. 2006. BLM Density Management and Riparian Buffer Study: Establishment Report and Study Plan. U.S. Geological Survey.
- Coley, P., Bryant, J., and Chapin III, F. 1985. Resource availability and plant antiherbivore defense. Science 230(4728): 895.
- D'Amato, A.W., Bradford, J.B., Fraver, S., and Palik, B.J. 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. Forest Ecology and Management 262: 803-816.
- Davis, L.R., and Puettmann, K.J. 2009. Initial response of understory vegetation to three alternative thinning treatments. Journal of Sustainable Forestry 28(8): 904-934.
- Davis, M.A., Grime, J.P., and Thompson, K. 2000. Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology 88(3): 528-534.
- Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., De Foucault, B., Delelis-Dusollier, A., and Bardat, J. 2004. Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. Journal of Applied Ecology 41(6): 1065-1079.
- Diaz, S., and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16(11): 646-655.

- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M.R. 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg. Sci. 15(3): 295-304.
- Drever, C.R., and Lertzman, K.P. 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. Canadian Journal of Forest Research 31(12): 2124-2133.
- Drever, C.R., and Lertzman, K.P. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research 33(1): 137-146.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., and Flannigan, M. 2006. Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36(9): 2285-2299.
- Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., and Norberg, J. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1(9): 488-494.
- Fahey, R.T., and Puettmann, K.J. 2007. Ground layer disturbance and initial conditions influence gap partitioning of understorey vegetation. Journal of Ecology 95(5): 1098-1109.
- Fahey, R.T., and Puettmann, K.J. 2008. Patterns in spatial extent of gap influence on understory plant communities. Forest Ecology and Management 255(7): 2801-2810.
- Farji-Brener, A.G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. Oikos 92(1): 169-177.
- Fenner, M., Hanley, M.E., and Lawrence, R. 1999. Comparison of seedling and adult palatability in annual and perennial plants. Functional Ecology 13(4): 546-551.
- Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C.S., and Walker, B. 2002. Resilience and sustainable development: Building adaptive capacity in a world of transformations. Ambio 31(5): 437-440.

- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35: 557-581.
- Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Chapin, T., and Rockström, J. 2010. Resilience thinking: integrating resilience, adaptability and transformability. Ecology and Society 15(4): 20.
- Franklin, J.F. 1993. Lessons from old-growth: Fueling controversy and providing direction. Journal of Forestry 91: 10-13.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., and Golodets, C. 2007. Assessing the effects of landuse change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. Annals of Botany 99(5): 967.
- Gilkey, H.M., and Dennis, L.J. 2001. Handbook of Northwestern plants. Oregon State University Press, Corvallis, OR.
- Gilliam, F.S., and Roberts, M.R. 2003. The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, USA.
- Gray, A.N., and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78(8): 2458-2473.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242(5396): 344-347.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111(982): 1169-1194.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86(6): 902-910.
- Gunderson, L.H. 2000. Ecological resilience in theory and application. Annu. Rev. Ecol. Syst. 31: 425-439.
- Hagar, J., Howlin, S., and Ganio, L. 2004. Short-term response of songbirds to experimental thinning of young Douglas-fir forests in the Oregon Cascades. Forest Ecology and Management 199(2-3): 333-347.
- Hagar, J.C. 2007a. Key elements of stand structure for wildlife in production forests west of the Cascade Mountains. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-695.

- Hagar, J.C. 2007b. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. Forest Ecology and Management 246(1): 108-122.
- Halaj, J., Ross, D.W., and Moldenke, A.R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90(1): 139-152.
- Hale, S.E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. Forest Ecology and Management 179(1-3): 341-349.
- Halpern, C.B. 1989. Early successional patterns of forest species interactions of life-history traits and disturbance. Ecology 70(3): 704-720.
- Halpern, C.B., McKenzie, D., Evans, S.A., and Maguire, D.A. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecological Applications 15(1): 175-195.
- Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5(4): 913-934.
- Hamilton, E.H., and Haeussler, S. 2008. Modeling stability and resilience after slashburning across a sub-boreal to subalpine forest gradient in British Columbia. Canadian Journal of Forest Research 38(2): 304-316.
- Hanley, T.A., Spalinger, D.E., Mock, K.J., Weaver, O.L., and Harris, G.M. 2012. Forage resource evaluation system for habitat—deer: an interactive deer habitat model. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-858.
- Harrington, C.A., Buermeyer, K.R., Brodie, L.C., and Wender, B.W. 2002. Factors influencing growth and flowering of understory plants in conifer stands in western Washington. In. US Dept. of Agriculture, Forest Service, Pacific Northwest Research Station. p. 159.
- Harrington, T.B., and Edwards, M.B. 1999. Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations. Canadian Journal of Forest Research 29(7): 1055-1064.
- Harrison, G.W. 1979. Stability under environmental stress: Resistance, resilience, persistence, and variability. The American Naturalist 113(5): 659-669.
- Hayes, J.P., Weikel, J.M., and Huso, M.M.P. 2003. Response of birds to thinning young Douglas-fir forests. Ecological Applications 13(5): 1222-1232.
- Heithecker, T.D., and Halpern, C.B. 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management 226(1-3): 60-71.

- Hitchcock, C.L., and Cronquist, A. 2001. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.
- Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1-23.
- Holling, C.S. 1996. Engineering resilience versus ecological resilience. In Engineering within Ecological Constraints. Edited by P. C. Schulze. National Academy Press, Washington, D. C.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75(1): 3-35.
- Huffman, D.W., Tappeiner II, J.C., and Zasada, J.C. 1994. Regeneration of salal (Gaultheria shallon) in the central Coast Range forests of Oregon. Canadian Journal of Botany 72(1): 39-51.
- Hughes, J.W., and Fahey, T.J. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. Journal of Ecology 79(3): 605-616.
- Jordano, P. 2000. Fruits and frugivory. In Seeds: The Ecology of Regeneration in Plant Communities. Edited by M. Fenner. CABI Publ., Wallingford, UK. pp. 125-166.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bonisch, G., Garnier, E., Westboy, M., Reich, P.B., and Wright, I.A. 2011. TRY—a global database of plant traits. Global Change Biology 17(9): 2905-2935.
- Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3(2): 157-164.
- Klinka, K., Chen, H.Y.H., Wang, Q., and De Montigny, L. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on west Vancouver Island. Northwest Science 70(3): 193-200.
- Lavorel, S., Díaz, S., Cornelissen, J., Garnier, E., Harrison, S., McIntyre, S., Pausas, J., Pérez-Harguindeguy, N., Roumet, C., and Urcelay, C. 2007. Plant functional types: are we getting any closer to the Holy Grail? In Terrestrial Ecosystems in a Changing World. Edited by Josep G. Canadell, Diane E. Pataki, and Louis F. Pitelka. pp. 149-164.
- Lavorel, S., and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16(5): 545-556.

- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J., Pellet, G., and Douzet, R. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. Journal of Ecology 99: 135-147.
- Lavorel, S., McIntyre, S., Landsberg, J., and Forbes, T.D.A. 1997. Plant functional classifications: From general groups to specific groups based on response to disturbance. Trends in Ecology & Evolution 12(12): 474-478.
- Lindh, B., and Muir, P. 2004. Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? Forest Ecology and Management 192(2-3): 285-296.
- Lindh, B.C. 2008. Flowering of understory herbs following thinning in the western Cascades, Oregon. Forest Ecology and Management 256(5): 929-936.
- MacDonald, R.L., Burke, J.M., Chen, H.Y.H., and Prepas, E.E. 2012. Relationship between aboveground biomass and percent cover of ground vegetation in Canadian Boreal Plain riparian forests. Forest Science 58(1): 47-53.
- Manning, T., Hagar, J.C., and McComb, B.C. 2012. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. Forest Ecology and Management 264(0): 115-124.
- Martin, K.J., and McComb, W.C. 2002. Small mammal habitat associations at patch and landscape scales in Oregon. Forest Science 48(2): 255-264.
- McComb, W.C., McGarigal, K., and Anthony, R.G. 1993. Small mammal and amphibian abundace in streamside and upslope habits of mature Douglas-fir stands. Northwest Science 67(1): 7-15.
- McDowell, N., Brooks, J., Fitzgerald, S., and Bond, B. 2003. Carbon isotope discrimination and growth response of old Pinus ponderosa trees to stand density reductions. Plant, Cell & Environment 26(4): 631-644.
- McIntyre, S., Díaz, S., Lavorel, S., and Cramer, W. 1999. Plant functional types and disturbance dynamics Introduction. J. Veg. Sci. 10(5): 603-608.
- McKenzie, D., Halpern, C.B., and Nelson, C.R. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, USA. Canadian Journal of Forest Research 30(10): 1655-1666.
- McLeod, K., and Leslie, H. 2009. Ecosystem-Based Management for the Oceans. Cambridge Univ Press.
- Messier, C., and Puettmann, K.J. 2011. Forests as complex adaptive systems: Implications for forest management and modelling. Italian Journal of Forest and Mountain Environments 66(3): 249-258.

- Mori, A.S. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48(2): 280-292.
- Mote, P., Salathé, E., Duilére, V., and Jump, E. 2008. Scenarios of Future Climate for the Pacific Northwest. University of Washington.
- Muir, P.S., Mattingly, R.L., Tappeiner, J.C., Bailey, J.D., Elliott, W.E., Hagar, J.C., Miller, J.C., Peterson, E.B., and Starkey, E.E. 2002. Managing for biodiversity in young Douglas-fir forests of western Oregon. US Geological Survey, Forest and Rangeland Ecosystem Science Center.
- Muukkonen, P., Makipaa, R., Laiho, R., Minkkinen, K., Vasander, H., and Finér, L. 2006. Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. Silva Fennica 40(2): 231.
- Nagai, M., and Yoshida, T. 2006. Variation in understory structure and plant species diversity influenced by silvicultural treatments among 21-to 26-year-old Picea glehnii plantations. Journal of Forest Research 11(1): 1-10.
- Natureserve. 2010. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.0. NatureServe, Arlington, VA. U.S.A. Available http://www.natureserve.org/explorer. (Accessed: October 2010)
- Nelson, C.R., and Halpern, C.B. 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Canadian Journal of Botany 83(6): 610-620.
- Nelson, C.R., Halpern, C.B., and Agee, J.K. 2008. Thinning and burning result in low-level invasion by nonnative plants but neutral effects on natives. Ecol Appl 18(3): 762-770.
- Ninemets, Ü., and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76(4): 521-547.
- Norberg, J., and Cumming, G.S. (eds). 2008. Complexity Theory for a Sustainable Future. Columbia University Press, NY.
- Nyland, R.D. 2002. Silviculture: Concepts and Applications. 2nd ed. McGraw-Hill New York.
- Odion, D.C., and Sarr, D.A. 2007. Managing disturbance regimes to maintain biological diversity in forested ecosystems of the Pacific Northwest. Forest Ecology and Management 246(1): 57-65.
- Olsson, P., Folke, C., and Berkes, F. 2004. Adaptive comanagement for building resilience in social-ecological systems. Environmental Management 34(1): 75-90.

- Palik, B., Mitchell, R.J., Pecot, S., Battaglia, M., and Pu, M. 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. Ecological Applications 13(3): 674-686.
- Pastor, J., Light, S., and Sovell, L. 1998. Sustainability and resilience in boreal regions: sources and consequences of variability. Conservation Ecology [online] 2(2): 16.
- Petchey, O., and Gaston, K. 2009. Effects on ecosystem resilience of biodiversity, extinctions, and the structure of regional species pools. Theoretical Ecology 2(3): 177-187.
- Peterson, G., Allen, C.R., and Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1(1): 6-18.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and Team, R.D.C. 2011. nlme: Linear and Nonlinear Mixed Effects Models.
- Poage, N.J., and Anderson, P.D. 2007. Large-scale silviculture experiments fo western Oregon and Washington. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-713.
- Pojar, J., and Mackinnon, A. 1994. Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia, and Alaska. Lone Pine Publishing, Redmond, OR.
- Puettmann, K.J. 2011. Silvicultural challenges and options in the context of global change: Simple fixes and opportunities for new management approaches. Journal of Forestry 109(6): 321-331.
- Puettmann, K.J., Coates, K.D., and Messier, C. 2009. A Critique of Silviculture: Managing for Complexity. Island Press, Washington, DC.
- R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raunkiær, C. 1934. Life forms of plants and statistical plant geography. Arno Press.
- Reich, P.B., Frelich, L.E., Voldseth, R.A., Bakken, P., and Adair, C. 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. Journal of Ecology: no-no.
- Roberts, M. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Botany 82(9): 1273-1283.

- Roberts, M., and Zhu, L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. Forest Ecology and Management 155(1-3): 17-31.
- Roberts, M.R., and Gilliam, F.S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. Ecological Applications 5(4): 969-977.
- Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In The Role of Fire in Northern Circumpolar Ecosystems. Edited by Wein R. W., and MacLean D. A. John Wiley & Sons Ltd. pp. 135-154.
- Sack, L., Grubb, P.J., and Marañón, T. 2003. The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. Plant Ecology 168(1): 139-163.
- Scheller, R.M., and Mladenoff, D.J. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. Ecological Applications 12(5): 1329-1343.
- Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. Forest Ecology and Management 78(1-3): 115-125.
- Smith, T., and Huston, M. 1989. A theory of the spatial and temporal dynamics of plant communities. Plant Ecology 83(1): 49-69.
- Spies, T.A., and Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggiero L.F., Aubry K.B., Carey A.B., Huff M.H. tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Stewart, R.E. 1975. Allelopathic potential of western bracken. Journal of Chemical Ecology 1(2): 161-169.
- Suding, K.N., Goldberg, D.E., and Hartman, K.M. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84(1): 1-16.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., and Navas, L. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14(5): 1125-1140.
- Suzuki, Nobuya, Hayes, and John, P. 2003. Effects of thinning on small mammals in Oregon Coastal Forests. Anglais 67: 352-371.

- Tappeiner, J.C., Zasada, J.C., Huffman, D.W., and Ganio, L.M. 2001. Salmonberry and salal annual aerial stem production: the maintenance of shrub cover in forest stands. Canadian Journal of Forest Research 31(9): 1629-1638.
- The Calflora Database. 2010. Calflora: Information on California plants for education, research and conservation. [web application]. 2008. Berkeley, California: The Calflora Database [a non-profit organization]. Available: http://www.calflora.org/ (Accessed: Oct 11, 2010).
- Thomas, J.W., Franklin, J.F., Gordon, J., and Johnson, K.N. 2006. The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. Conservation Biology 20(2): 277-287.
- Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., and Austin, K.A. 1999. Plant diversity in managed forests: Understory responses to thinning and fertilization. Ecological Applications 9(3): 864-879.
- Thompson, I., Mackey, B., McNulty, S., and Mosseler, A. 2009. Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecoystems. Secretariat of the Convention on Biological Diversity. CBD Technical Series no. 43.
- Thysell, D., and Carey, A. 2000. Effects of forest management on understory and overstory vegetation: A retrospective study. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-488.
- Thysell, D.R., and Carey, A.B. 2001. Manipulation of density of Pseudotsuga menziesii canopies: preliminary effects on understory vegetation. Canadian Journal of Forest Research 31(9): 1513-1525.
- USDA-Forest Service. 2010. Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis [2010, October 11].
- USDA-NRCS. 2010. The PLANTS Database (http://plants.usda.gov, 27 August 2010). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- Vance, N.C., and Thomas, J. (eds). 1997. Special forest products: biodiversity meets the marketplace. U.S. Department of Agriculture, Forest Service, General Technical Report WO-GTR-063, Washington, DC.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. 2007. Let the concept of trait be functional! Oikos 116(5): 882-892.

- Vlok, J., and Yeaton, R. 2000. The effect of short fire cycles on the cover and density of understorey sprouting species in South African mountain fynbos. Diversity and Distributions 6(5): 233-242.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology 9(4): 747-752.
- Walker, B., Holling, C.S., Carpenter, S.R., and Kinzig, A. 2004. Resilience, adaptability and transformability in social–ecological systems. Ecology and Society 9(2): 5. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art5.
- Walker, B., Kinzig, A., and Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2(2): 95-113.
- Walker, B.H. 1992. Biodiversity and ecological redundancy. Conservation Biology 6(1): 18-23.
- Walker, B.H., Abel, N., Anderies, J.M., and Ryan, P. 2009. Resilience, adaptability, and transformability in the Goulburn-Broken Catchment, Australia. Ecology and Society 14(1): 12.
- Warren, R.J. 2008. Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position. Plant Ecology 198(2): 297-308.
- Weiher, E., Adrie, W., Ken, T., Michael, R., Eric, G., and Ove, E. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. J. Veg. Sci. 10(5): 609-620.
- Wender, W., B., Harrington, A., C., Tappeiner, and C., J. 2004. Flower and fruit production of understory shrubs in western Washington and Oregon. Northwest Science 78(2): 17.
- Wessell, S.J. 2005. Biodiversity in managed forests of western Oregon: Species assemblages in leave islands, thinned, and unthinned forests. In Wildlife Science. Oregon State University, Corvallis, OR. p. 161.
- Western Regional Climate Center. 2007. California climate summaries. Available from http://www.wrcc.dri.edu/COMPARATIVE.htmlAccessed 2011].
- Wilson, D.S., Anderson, P.D., and Puettmann, K.J. 2009. Evaluating the consistency of understorey vegetation response to forest thinning through synthetic analysis of operational-scale experiments. Forestry 82(5): 583-596.
- Wilson, D.S., and Puettmann, K.J. 2007. Density management and biodiversity in young Douglas-fir forests: Challenges of managing across scales. Forest Ecology and Management 246(1): 123-134.

- Yi, H., and Moldenke, A. 2005. Response of ground-dwelling arthropods to different thinning intensities in young Douglas-fir forests of western Oregon. Environmental entomology 34(5): 1071-1080.
- Zenner, E.K., Kabrick, J.M., Jensen, R.G., Peck, J.E., and Grabner, J.K. 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. Forest Ecology and Management 222(1-3): 326-334.

FIGURES

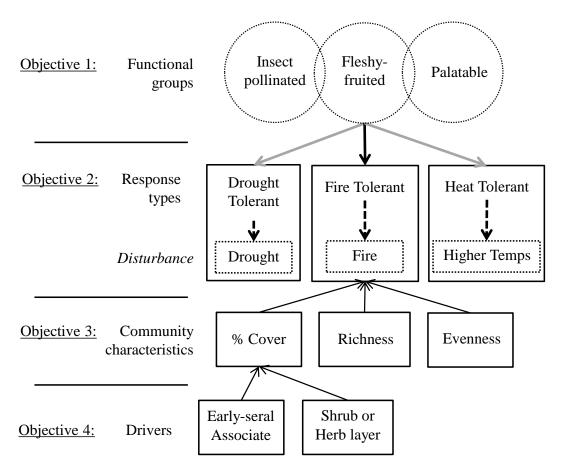


Figure 1. Conceptual model of the research structure and species groups being evaluated for each objective. By focusing on plant traits that relate to ecosystem functions and their ability to respond to changes the impacts of thinning on the resilience of these functions can be assessed. As an example, this model describes the flow of objectives for the fleshy-fruited functional group in the top tier to the second tier, which sorts species by the similarity of response to the specific disturbance, in this case fire tolerance. The bottom tiers examine the community characteristics and drivers responding to thinning and directing changes in resilience. (Adapted from Puettmann 2011)

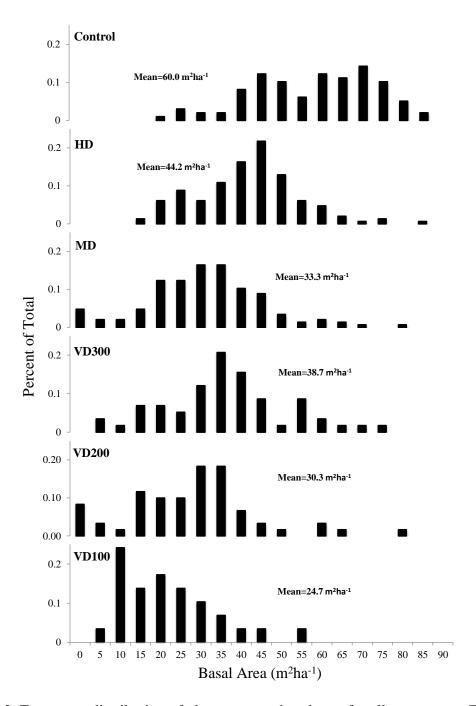


Figure 2. Frequency distribution of plot overstory basal area for all treatments. Even though treatments were thinned to target densities there is a large degree of overlap among treatments and unthinned controls. CON=control, HD=high density retention, MD=moderate density retention, VD=variable density retention to 300, 200, and 100 TPH.

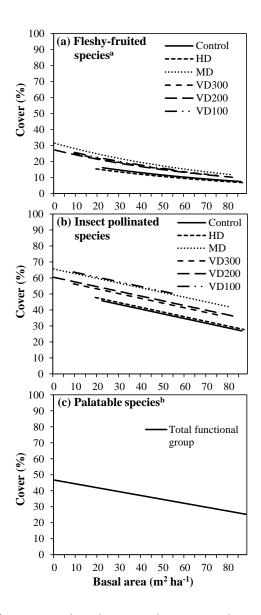


Figure 3. Relationship of overstory basal area and mean total cover of fleshy-fruited species (a), insect pollinated species (b), and palatable species (c) in the unthinned control and thinning treatments. CON=control, HD=high density retention, MD=moderate density retention, VD=variable density retention to 300, 200, and 100 TPH.

^a Total cover of fleshy-fruited plants was log(Y+1) transformed prior to regression analysis. ^b model that did not distinguish differences in the cover-basal area relationships between treatments and the unthinned control for palatable species was best supported by the data.

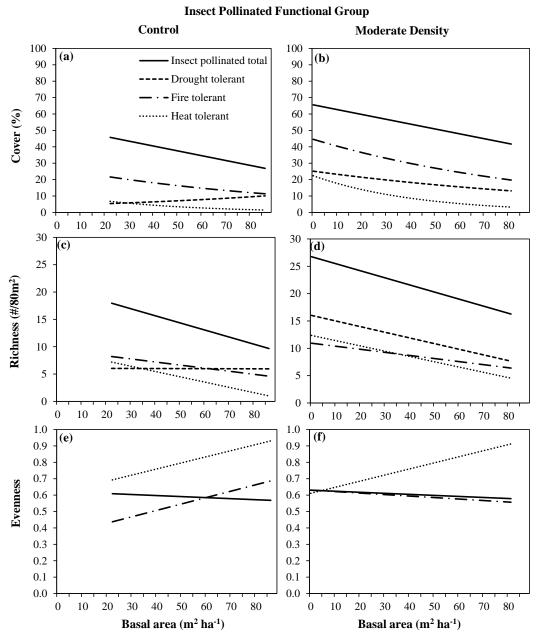


Figure 4. Insect pollinated functional group and response type cover (a and b), richness (c and d) and evenness (e and f) along a basal area gradient for the control (left column) and moderate density treatment (right column).

Model that did not distinguish differences in the evenness-basal area relationships for the drought tolerant response type was best supported by the data, i.e., the null model was the best supported model using AIC_c; therefore, it was not represented.

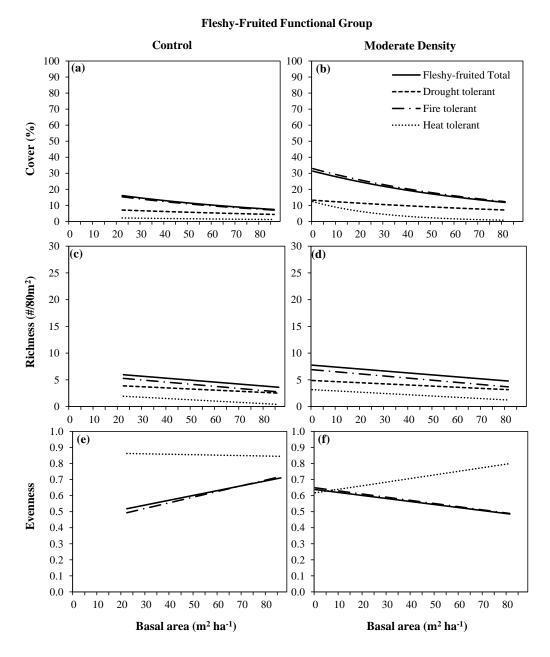


Figure 5. Fleshy-fruited functional group and response type cover (a and b), richness (c and d) and evenness (e and f) along a basal area gradient for the control (left column) and moderate density treatment (right column).

Model that did not distinguish differences in the evenness-basal area relationships for the drought tolerant response type was best supported by the data, i.e., the null model was the best supported model using AIC_c; therefore, it was not represented.

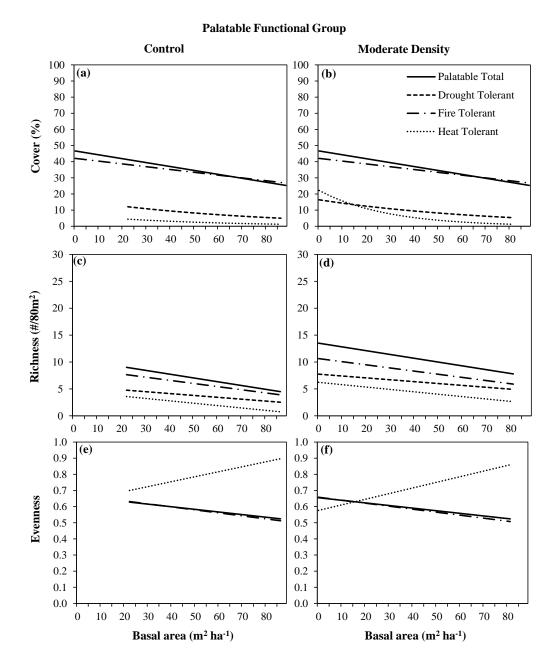


Figure 6. Palatable functional group and response type cover (a and b), richness (c and d) and evenness (e and f) along a basal area gradient for the control (left column) and moderate density treatment (right column).

Model that did not distinguish differences in the evenness-basal area relationships for the drought tolerant response type was best supported by the data, i.e., the null model was the best supported model using AIC_c; therefore, it was not represented.

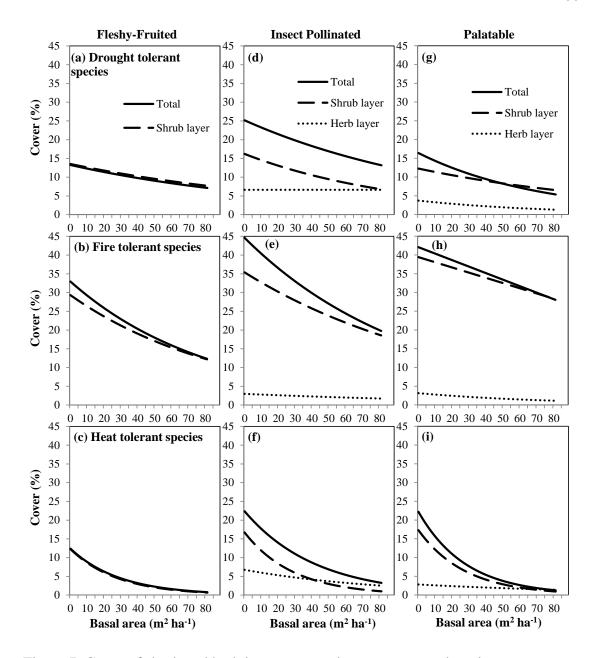


Figure 7. Cover of shrub and herb layer structural components and total response type group cover relationships to overstory basal area for the insect pollinated (a, b and c), fleshy-fruited (d, e and f) and palatable (g, h and i) functional groups in the moderate density treatment. The relationship between cover of the herb layer for the response types in fleshy-fruited functional group was not supported by the data.

Control **Moderate Density** (a) Drought tolerant species (b) Drought tolerant species Total Total Cover (%) Early Seral Early seral (c) Fire tolerant species (d) Fire tolerant species Cover (%) 30 40 50 30 40 (f) Heat tolerant species (e) Heat tolreant species 30 40 50 70 80 40 50 Basal area (m² ha-1) Basal area (m² ha⁻¹)

Insect Polinated Functional Group

Figure 8. Cover of early seral species and total response type group in the control (a, c and e) and moderate density treatment (b, d and f) along a basal area gradient for the insect pollinated functional group. Similar figures for the fleshy-fruited and palatable functional groups are presented in Appendix E.

TABLES

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

| | D . # P | D.1.1. C1 | C D 1 | IZ 1 M | NI d - C | OMILLL | T II'.1 |
|---|---------------|---------------|---------------|--------------------|---------------|----------------------------|----------------------------|
| | Bottomline | Delph Creek | Green Peak | Keel Mountain | North Soup | OM Hubbard | Ten High |
| Ecological Province | Coast Range | Cascade Range | Coast Range | Cascade Range | Coast Range | Coast Range | Coast Range |
| Latitude | N43°46'20.0" | N45°15'56.0" | N44°22'00.0" | N44°31'41.0" | N43°33'57.0" | N43°17'30.0" | N44°16'50.0" |
| Longitude | W123°14'11.0" | W122°09'33.0" | W123°27'30.0" | W122°37'55.0" | W123°46'38.0" | W123°35'00.0" | W123°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 | Sept.1997 | Apr. 2000 | Jan. 2000 | Dec. 1997 | Aug. 1998 | Sept. 1997 | April 1998 to Mar. 2000 |
| Stand age at harvest | 55 | 53 | 56 | 44 | 48 | 39 | 44 |
| Site index at yr 50 (m) (King 1966) | 42 | 37 | 37 | 39 | 40 | 36 | 38 |
| Mean Annual Precip. (mm) ^b | 1299 | 1897 | 2121 | 1968 | 1735 | 1417 | 2726 |
| Mean Annual Summertime max Temp. (C°) 1994-2007 ^b | 26.8 | 23.6 | 26.1 | 23.9 | 25.5 | 24.8 | 25.1 |
| | HD: C | HD: C | HD: C | HD: C | HD: C | HD: C, G | HD: C |
| Harvesting method ^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 & 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 For. conservation Genetics, http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA_web/, accessed 25 Jan 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=Pre-commertial thin.

Table 2. Treatment summary for the DMS sites.

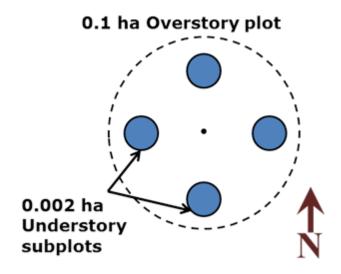
| Thinning treatment | Target tree density (TPH) | Area thinned (% treatment area) | Thinning pattern |
|---|---------------------------------|---------------------------------|--|
| Unthinned control (CON) (~16-25 ha) | 500-860 | 0 | - |
| High density retention (HD) (~14-35 ha) | 300 | 70-75 | 3-14% left unthinned in circular leave islands up to 1 acre |
| Moderate density retention (MD) (~23-69 ha) | 200 | 60-65 | 3-11% left unthinned in circular leave islands up to 1 acre 3-10% of stand cut in circular patch openings up to 1 acre |
| Variable density retention (~20-39 total) | | | 1-3% left unthinned in circular leave islands |
| (VD100) | 100 | 10-30 | up to 1 acre |
| (VD200) | 200 | | 2-4% of stand cut in circular patch openings |
| (VD300) | 300 | | up to 1 acre |

Table 3. Dominant species (in terms of % cover) and their functional and response type group contribution. X=contributes to the functional group or response type. UNK=unknown contribution.

| | | | | | | Fu | nctional gr | oups | Res | ponse ty | pes |
|---|------------------------|-----------------------------|----------------------|------|-------|--------------------|-------------------|-----------|---------------------|----------|------------------|
| Scientific name | Common name | Mean cover when present (%) | Mean cover (%) | | Freq. | Fleshy- fruited | Insect pollinated | Palatable | Drought tolerant | | Heat tolerant |
| Polystichum munitum (Kaulf.) C. Presl | western swordfern | 15.61 | 15.20 | | 1 | | | X | | X | |
| Gaultheria shallon Pursh | salal | 13.35 | 10.12 | 0.76 | 4 | X | X | | | X | |
| Acer circinatum Pursh | vinemaple | 12.09 | 5.42 | 0.45 | 14 | | X | X | | X | |
| Mahonia nervosa (Pursh) Nutt. | Oregon grape | 6.49 | 4.34 | 0.67 | 8 | X | X | X | X | X | |
| Pteridium aquilinum (L.) Kuhn | western brackenfern | 4.88 | 3.56 | 0.73 | 7 | | | | X | X | X |
| Oxalis oregana Nutt. | redwood-sorrel | 9.06 | 3.43 | 0.38 | 20 | | X | UNK | X | UNK | |
| Rubus ursinus Cham. & Schltdl. | trailing blackberry | 2.59 | 2.37 | 0.92 | 2 | X | X | X | X | X | X |
| Corylus cornuta var. californica Marsh. | california hazel | 7.82 | 2.03 | 0.26 | 31 | | | | | X | |
| Vaccinium parvifolium Sm. | red huckleberry | 2.72 | 2.02 | 0.74 | 5 | X | X | X | X | X | |
| Whipplea modesta Torr. | common whipplea | 5.17 | 1.68 | 0.33 | 23 | | X | UNK | X | UNK | |

APPENDICES

APPENDIX A. PLOT SAMPLING DIAGRAM



Appendix A. Sampling schematic for the vegetation survey showing the 0.1 ha overstory plot and the four 0.002 ha understory plots. Diagram modified from Harmon and Sexton (1996).

APPENDIX B. SPECIES LIST AND CHARACTERISTICS USED IN THIS STUDY.

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|---------------------------|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Acer circinatum | No ³ | Yes | Mod. ¹ | Low ¹ | Yes ¹ | No | Shrub | L |
| Achillea millefolium | No^3 | Yes | Mod. ¹ | Mod. ¹ | Yes^2 | Yes | Herb | E |
| Achlys triphylla | No^3 | Yes | High ¹⁵ | Low | Unk | No | Herb | L |
| Actaea rubra | Yes ³ | Yes ³ | Mod. | Low | Yes^2 | Yes | Herb | L |
| Adenocaulon bicolor | No^3 | Yes | Unk | Low | Unk | No | Herb | L |
| Adiantum aleuticum | No | No | Unk | Low | Unk | Yes | Shrub | L |
| Agoseris sp. | No^3 | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Agoseris grandiflora | No^3 | Yes | Low ¹ | Mod. ¹ | Unk | Yes | Herb | E |
| Agrostis sp. | No | No | Unk | Low | Unk | Yes | Herb | Unk |
| Agrostis capillaris | No | No | Low ¹ | Low^1 | Unk | No | Herb | Unk |
| Agrostis exarata | No | No | Mod. ¹ | Low ¹ | Yes ² | Yes | Herb | F |
| Agrostis gigantea | No | No | $High^1$ | Low^1 | Yes^2 | Yes | Herb | E |
| Agrostis scabra | No | No | Mod. ¹ | Low^1 | No^2 | Yes | Herb | F |
| Aira caryophyllea | No | No | Unk | High ³ | No | Yes | Herb | Unk |
| Allotropa virgata | No^3 | Yes | Unk | $Mod.^3$ | Unk | No | Herb | L |
| Amelanchier alnifolia | Yes^3 | Yes | Mod. ¹ | Low^1 | Yes ¹ | Yes | Shrub | Unk |
| Anaphalis margaritacea | No ³ | Yes | Low ¹ | Mod. ¹ | Unk | Yes | Herb | E |
| Anemone deltoidea | No^4 | Yes | low^{15} | Low^3 | Unk | No | Herb | L |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|------------------------------|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Anemone lyallii | No^4 | Yes | Unk | Low ⁸ | Unk | No | Herb | Unk |
| Angelica arguta | No^3 | Yes | High ¹² | Low^1 | Unk | No | Herb | Unk |
| Antennaria howellii | No^3 | Yes | Unk | Mod. ⁸ | Unk | No | Herb | Unk |
| Antennaria racemosa | No^3 | Yes | $Mod.^2$ | Mod. ³ | No^2 | No | Herb | Unk |
| Aquilegia formosa | No^4 | Yes | High ¹ | Mod. ¹ | Yes ² | Yes | Herb | E |
| Arctostaphylos columbiana | Yes ³ | Yes | Low^1 | Low ¹ | No^2 | No | Shrub | F |
| Asarum caudatum | No | Yes | $Mod.^2$ | Low^3 | Yes^2 | No | Herb | L |
| Asyneuma prenanthoides | No | Yes | Unk | Mod. | Unk | No | Herb | E/L |
| Athyrium filix-femina | No | No | $Mod.^2$ | Low^1 | Yes ² | Yes | Shrub | E |
| Blechnum spicant | No | No | High ¹² | Low^1 | Yes^2 | No | Shrub | L |
| Boschniakia strobilacea | No^3 | Yes | Unk | Mod. ⁹ | Unk | Yes | Herb | L |
| Boykinia major | No^3 | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Boykinia occidentalis | No^3 | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Brachypodium sylvaticum | No | No | Unk | High ¹⁰ | Unk | No | Herb | Unk |
| Bromus sp. | No | No | Unk | Mod. | Unk | Yes | Herb | Unk |
| Bromus carinatus | No | No | $High^1$ | $Mod.^1$ | No^2 | Yes | Herb | E |
| Bromus tectorum | No | No | Low^7 | High ⁷ | No | Yes | Herb | F |
| Bromus vulgaris | No | No | $Mod.^1$ | $High^1$ | Yes^2 | No | Herb | F |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|--|--------------------|-------------------|------------------|---------------------------|------------------|------------------|---------|-----------------------------------|
| Calypso bulbosa | No ³ | Yes | Low ² | Low ² | Yes ² | No | Herb | E/L |
| Campanula scouleri | No | Yes | Unk | Mod. ³ | Unk | No | Herb | E |
| Cardamine | No | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Cardamine angulata | No | Yes | Unk | Low^3 | Unk | No | Herb | E |
| Carex sp. | No^3 | No | Unk | Mod. | Unk | Yes | Herb | Unk |
| Carex deweyana | No^3 | No | Low^1 | $\operatorname{Mod.}^{1}$ | Unk | No | Herb | Unk |
| Carex hendersonii | No^3 | No | Low^1 | Low^1 | Unk | No | Herb | Unk |
| Carex mertensii | No^3 | No | Low^1 | Mod. ¹ | Unk | No | Herb | Unk |
| Carex rossii | No^3 | No | Low^1 | \mathbf{High}^1 | Yes^2 | Yes | Herb | E |
| Ceanothus velutinus | No^3 | Yes | Low^1 | Low^1 | Yes ¹ | No | Shrub | E |
| Cephalanthera austiniae | No^3 | Yes | Unk | Mod. ⁸ | Unk | Yes | Herb | L |
| Cerastium arvense | No^5 | Yes | Unk | $High^3$ | Unk | No | Herb | E |
| Cerastium fontanum ssp. vulgare | No ⁵ | Yes | Unk | Mod. ⁸ | Unk | No | Herb | Unk |
| Chamerion angustifolium | No | Yes | $High^2$ | Low | Yes ² | Yes | Herb | Е |
| Chamerion angustifolium ssp. angustifolium | No | Yes | $High^2$ | Low ¹ | Yes ² | No | Herb | Е |
| Chimaphila menziesii | No^3 | Yes | Low^2 | Mod. ³ | Yes ² | Yes | Shrub | L |
| Chimaphila umbellata | No^3 | Yes | Low^2 | Mod. ¹ | No^2 | Yes | Shrub | L |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|--|--------------------|-------------------|------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Chrysolepis chrysophylla var. chrysophylla | No ³ | No | Low ¹ | High ¹ | Yes ¹ | No | Shrub | E |
| Chrysosplenium glechomifolium | No^3 | Yes | Unk | Low ⁸ | Unk | No | Herb | Unk |
| Circaea alpina | No | Yes | Mod. 12 | Low^1 | Unk | Yes | Herb | E |
| Cirsium sp. | No^3 | Yes | Unk | High | Unk | Yes | Herb | Unk |
| Cirsium arvense | No^3 | Yes | Low^2 | $High^2$ | Yes ² | Yes | Herb | E |
| Cirsium brevistylum | No^3 | Yes | Low | Low^8 | No | Yes | Herb | Unk |
| Cirsium vulgare | No^3 | Yes | Low^2 | $High^2$ | No^2 | Yes | Herb | E |
| Claytonia perfoliata | No | Yes | Low^1 | Low^1 | No | Yes | Herb | F |
| Claytonia sibirica | No | Yes | Low | Low^1 | No | No | Herb | L |
| Claytonia sibirica var. sibirica | No | Yes | Low ¹ | Low ¹ | No | No | Herb | L |
| Clinopodium douglasii | No^3 | Yes | Unk | Mod. ⁸ | Unk | No | Herb | E |
| Collomia heterophylla | No^5 | Yes ⁵ | Unk | High ³ | No | No | Herb | E |
| Coptis laciniata | No^3 | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Corallorhiza maculata | No^3 | Yes | Unk | $Mod.^3$ | Unk | Yes | Herb | L |
| Corallorhiza striata | No^3 | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Cornus nuttallii | Yes ² | Yes ² | Low^1 | Low^1 | Yes ¹ | Yes | Shrub | L |
| Corylus cornuta var. californica | No ³ | No | Low ¹ | Low ¹ | Yes ¹ | No | Shrub | Е |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|----------------------------------|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Crepis sp. | No ³ | Yes | Unk | High | Unk | Yes | Herb | Unk |
| Crepis capillaris | No^3 | Yes | Low^1 | High ³ | No | Yes | Herb | L |
| Crepis setosa | No^3 | Yes | Low^1 | High ³ | No | No | Herb | Unk |
| Cynosurus sp. | No | No | Unk | High | Unk | Yes | Herb | Unk |
| Cynosurus cristatus | No | No | High ¹⁷ | Low ¹⁷ | No^{17} | No | Herb | Unk |
| Cynosurus echinatus | No | No | Low | High | No | Yes | Herb | Unk |
| Cytisus scoparius | No^3 | Yes | Low ¹ | High ¹ | Yes ² | No | Shrub | E |
| Dactylis glomerata | No | No | $Mod.^1$ | $Mod.^1$ | Yes^2 | Yes | Herb | F |
| Deschampsia cespitosa | No | No | $Mod.^2$ | Low^2 | Yes^2 | Yes | Herb | E |
| Deschampsia elongata | No | No | Low^1 | Mod. ¹ | Yes ² | Yes | Herb | F |
| Dicentra formosa | No^3 | Yes | Low ¹ | Low^1 | Unk | No | Herb | L |
| Dicentra formosa ssp. oregona | No^3 | Yes | Low ¹ | Low ¹ | Unk | No | Herb | L |
| Digitalis purpurea | No^3 | Yes | Low^1 | Low^1 | Unk | Yes | Herb | E |
| Dryopteris arguta | No^3 | No | Unk | $Mod.^3$ | Unk | Yes | Shrub | Unk |
| Dryopteris expansa | No^3 | No | Unk | Low^3 | Unk | No | Shrub | L |
| Elymus glaucus | No^3 | No | Low^1 | \mathbf{High}^1 | Yes ² | Yes | Herb | E |
| Elymus glaucus ssp. jepsonii | No | No | Low | High ¹ | Yes ² | Yes | Herb | E |
| Epilobium sp. | No | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Epilobium brachycarpum | No | Yes | Unk | High ³ | No | Yes | Herb | E |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|--------------------------------------|--------------------|-------------------|-------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Epilobium ciliatum | No | Yes | Unk | Mod. ³ | Unk | Yes | Herb | Е |
| Epilobium minutum | No | Yes | Unk | Mod. ³ | No | Yes | Herb | Е |
| Equisetum arvense | No^3 | No | Low^1 | Low^2 | Yes^2 | Yes | Herb | Е |
| Equisetum telmateia var. braunii | No^3 | No | Low ¹ | Low ² | Yes ² | Yes | Herb | Е |
| Erechtites minima | No^3 | Yes | Unk | Mod. ⁴ | No | No | Herb | E |
| Erodium cicutarium | No^3 | Yes | \mathbf{High}^7 | \mathbf{High}^7 | No | Yes | Herb | E |
| Festuca sp. | No | No | Unk | Mod. | Unk | Yes | Herb | Unk |
| Festuca californica | No | No | $Mod.^1$ | $High^1$ | Yes^2 | No | Herb | F |
| Festuca idahoensis | No | No | Mod. ¹ | Low ¹ | Yes^2 | No | Herb | L |
| Festuca occidentalis | No | No | \mathbf{High}^1 | $High^1$ | Unk | No | Herb | Unk |
| Festuca rubra | No | No | Mod. ¹ | Mod. ¹ | Yes^2 | Yes | Herb | E |
| Festuca subulata | No | No | Low^1 | Low ¹ | Yes^2 | Yes | Herb | F |
| Festuca subuliflora | No | No | Unk | Low ³ | Unk | No | Herb | Unk |
| Fragaria sp. | Yes ³ | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Fragaria vesca | Yes ³ | Yes | $Mod.^2$ | Mod. ² | Yes^2 | Yes | Herb | Е |
| Fragaria vesca ssp. bracteata | Yes ³ | Yes | Mod. ² | Mod. ² | Yes ² | No | Herb | E |
| Fragaria virginiana ssp. platypetala | Yes ³ | Yes | Mod. ² | Mod. ² | Yes ² | Yes | Herb | E |
| Frangula purshiana | Yes^3 | Yes | Low | Mod. ¹ | Yes ¹ | No | Shrub | L |

| Accepted Scientific | Fleshy- | Insect | 5 1 . 1 . 1 . 1 | Drought | Fire | Heat | G | Seral |
|-----------------------------|------------------|------------|------------------------|-------------------|------------------|----------|----------|--------------------------|
| Name | fruited | pollinated | Palatability | Tolerance | tolerant | tolerant | Stratum | Association ^a |
| Galium aparine | No^3 | Yes | Low^2 | Low ¹ | No^2 | Yes | Herb | L |
| Galium oreganum | No^3 | Yes | Low ¹ | Low^1 | Unk | No | Herb | Unk |
| Galium trifidum | No^3 | Yes | Low^2 | Low^1 | Yes^2 | Yes | Herb | L |
| Galium triflorum | No^3 | Yes | Low^2 | Low^2 | Yes ² | Yes | Herb | L |
| Gamochaeta purpurea | No^3 | Yes | Unk | High ³ | No | Yes | Herb | Unk |
| Gaultheria shallon | Yes ³ | Yes | Low^1 | Low^1 | Yes ¹ | No | Shrub | L |
| Geranium sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Herb | Unk |
| Glechoma hederacea | No^3 | Yes | Low^2 | Low^2 | Unk | Yes | Herb | Unk |
| Gnaphalium sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Herb | E |
| Goodyera oblongifolia | No^3 | Yes | $Mod.^2$ | Low^2 | No^2 | No | Herb | L |
| Heuchera sp. | No^3 | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Heuchera micrantha | No^3 | Yes | Unk | High | Unk | No | Herb | Unk |
| Hieracium albiflorum | No^3 | Yes | Mod. ¹ | $High^1$ | Yes^2 | Yes | Herb | E |
| Hieracium scouleri | No^3 | Yes | Low^1 | ${\sf High}^1$ | Unk | No | Herb | Unk |
| Hierochloe occidentalis | No | No | Unk | Mod. ⁴ | Unk | No | Herb | Unk |
| Holcus lanatus | No | No | Low ¹ | $Mod.^1$ | Yes^2 | Yes | Herb | Unk |
| Holodiscus discolor | No^3 | Yes | Mod. ¹ | Low^1 | Yes ¹ | Yes | Shrub | E |
| Hydrophyllum occidentale | No^3 | Yes | Low^1 | Mod. ¹ | Unk | No | Herb | Unk |
| Hydrophyllum tenuipes | No^3 | Yes | Unk | Low ³ | Unk | No | Herb | Unk |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|-------------------------------------|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Hypericum perforatum | No ³ | Yes | Low ¹¹ | High ¹¹ | Unk | Yes | Herb | Е |
| Hypericum scouleri ssp. scouleri | No^3 | Yes | Unk | Low ³ | Unk | Yes | Herb | E |
| Hypochaeris glabra | No^3 | Yes | Unk | High ³ | No | Yes | Herb | Unk |
| Hypochaeris radicata | No^3 | Yes | High ¹⁶ | High ³ | Unk | No | Herb | E |
| Ilex sp. | Yes | Yes | Unk | Mod. | Yes | No | Shrub | E |
| Ilex aquifolium | Yes^3 | Yes | High | Mod. ¹⁸ | Yes | No | Shrub | E |
| Iris tenax | No^3 | Yes ³ | High ¹² | $Mod.^1$ | Unk | No | Herb | E/L |
| Juncus sp. | No^3 | No | Unk | Mod. | Unk | Yes | Herb | Unk |
| Juncus effusus | No^3 | No | $High^1$ | Mod. ¹ | Unk | Yes | Herb | E |
| Lactuca sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Herb | Unk |
| Lapsana communis | No^3 | Yes | Unk | Mod. ⁹ | No | No | Herb | E |
| Lathyrus sp. | No^3 | Yes ³ | Unk | Mod. | Unk | Yes | Herb | Unk |
| Lathyrus polyphyllus | No^3 | Yes | Low ¹² | Mod. ¹ | Unk | No | Herb | Е |
| Leptosiphon bolanderi | No^5 | Yes ⁵ | Unk | High ⁹ | No | No | Herb | Unk |
| Leucanthemum vulgare | No^3 | Yes | Low ¹ | Mod. ¹ | Unk | Yes | Herb | E |
| Lilium sp. | Unk | Yes | Unk | Unk | Unk | Yes | Herb | Unk |
| Lilium columbianum | No^3 | Yes | Unk | $Mod.^3$ | Unk | No | Herb | L |
| Linnaea borealis | No^3 | Yes | Low ¹³ | Mod. ³ | No^2 | No | Shrub | L |
| Linnaea borealis ssp. longiflora | No ³ | Yes | Low ¹⁵ | Mod. ³ | No^2 | No | Shrub | L |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|---|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Listera caurina | No ³ | Yes | Unk | Low ³ | Unk | No | Herb | L |
| Listera cordata | No^3 | Yes | Unk | Low ³ | Unk | No | Herb | L |
| Lolium perenne ssp. multiflorum | No | No | Low ¹ | Low ¹ | Yes ² | Yes | Herb | E |
| Lonicera sp. | Yes ³ | Yes | Unk | Mod. | Unk | Yes | Shrub | E |
| Lonicera ciliosa | Yes ³ | Yes | Low ¹³ | Mod. ³ | Unk | No | Shrub | F |
| Lonicera hispidula | Yes ³ | Yes | Low ¹³ | Mod. ³ | Unk | Yes | Shrub | E |
| Lotus sp. | No^3 | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Lotus crassifolius | No^3 | Yes | Low^1 | Low ¹ | Unk | Yes | Herb | E |
| Lotus crassifolius var. crassifolius | No^3 | Yes | Low ¹ | Low ¹ | Unk | Yes | Herb | E |
| Lotus denticulatus | No^3 | Yes | Unk | Mod. ³ | No | No | Herb | E |
| Lotus micranthus | No^3 | Yes | Unk | Mod. ³ | No | Yes | Herb | E |
| Lupinus sp. | No^3 | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Lupinus rivularis | No^3 | Yes | Unk | Mod. ⁴ | Unk | No | Herb | Unk |
| Luzula sp. | No^3 | No | Unk | Mod. | Unk | Yes | Herb | Unk |
| Luzula comosa | No^3 | No | Unk | Mod. ⁴ | Unk | Yes | Herb | Unk |
| Luzula parviflora | No^3 | No | Mod. ¹² | Low ¹ | Unk | Yes | Herb | E |
| Lysichiton americanus | Yes ³ | Yes ³ | Unk | Low^3 | Unk | No | Herb | E |
| Madia sp. | No^3 | Yes | Unk | High | Unk | Yes | Herb | Unk |
| Madia gracilis | No^3 | Yes | Unk | High ⁸ | No | Yes | Herb | E |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|---|--------------------|-------------------|-------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Madia madioides | No^3 | Yes | Unk | Mod. ⁸ | Unk | No | Herb | Е |
| Mahonia nervosa | Yes^3 | Yes | Mod. ¹ | $High^1$ | Yes ¹ | No | Shrub | L |
| Maianthemum dilatatum | Yes ³ | Yes | Unk | Low ⁸ | Unk | No | Herb | L |
| Maianthemum racemosum | Yes ³ | Yes | Unk | Low ⁸ | Unk | Yes | Herb | L |
| Maianthemum racemosum ssp. amplexicaule | Yes ³ | Yes | Unk | Low ⁸ | Unk | Yes | Herb | L |
| Maianthemum stellatum | Yes ³ | Yes | Unk | Low ⁸ | Unk | Yes | Herb | L |
| Marah oreganus | Yes | Yes | Unk | $Mod.^3$ | Unk | No | Herb | E |
| Melica | No | No | Unk | High | Unk | Yes | Herb | Unk |
| Melica bulbosa | No | No | High ¹ | High ¹ | Unk | Yes | Herb | Unk |
| Melica spectabilis | No | No | Mod. ¹ | $High^1$ | Unk | No | Herb | Unk |
| Melica subulata | No | No | Low^1 | Mod. ¹ | Unk | No | Herb | Unk |
| Mentha arvensis | No^3 | Yes | Low^1 | Low^1 | Unk | Yes | Herb | E |
| Mimulus dentatus | No^3 | Yes | Mod. 12 | Low^1 | Unk | No | Herb | Unk |
| Mitella sp. | No^3 | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Mitella ovalis | No^3 | Yes | Unk | Low ⁹ | Unk | No | Herb | L |
| Mitella pentandra | No^3 | Yes | Unk | Mod. ³ | Unk | No | Herb | Unk |
| Moehringia macrophylla | No^5 | Yes | Unk | Mod. ³ | Unk | No | Herb | E |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|---|--------------------|-------------------|--------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Monotropa hypopithys | No ³ | Yes | Unk | Mod. ³ | Unk | No | Herb | L |
| Monotropa uniflora | No^3 | Yes | Unk | Mod. ³ | Unk | No | Herb | L |
| Montia sp. | No | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Montia diffusa | No | Yes | Unk | Mod. ⁸ | No | No | Herb | L |
| Montia parvifolia ssp. parvifolia | No | Yes | Unk | Low ⁸ | Unk | No | Herb | Unk |
| Mycelis muralis | No^3 | Yes | Unk | $Mod.^3$ | No | No | Herb | E |
| Nemophila menziesii var. atomaria | No^3 | Yes | Unk | Mod. ³ | No | No | Herb | Unk |
| Nemophila parviflora | No^3 | Yes | Unk | $Mod.^3$ | No | No | Herb | E |
| Nemophila parviflora var. parviflora | No^3 | Yes | Unk | Mod. ³ | No | No | Herb | E |
| Oplopanax horridus | Yes ³ | Yes | $High^6$ | Low^2 | Yes ² | No | Shrub | L |
| Osmorhiza berteroi | No^3 | Yes | Mod. 15 | Mod. ³ | Unk | Yes | Herb | E |
| Oxalis oregana | No^3 | Yes | Unk | Mod. ³ | Unk | No | Herb | L |
| Oxalis suksdorfii | No^3 | Yes | Unk | Mod. ³ | Unk | No | Herb | E |
| Paxistima myrsinites | No^3 | Yes | $Mod.^2$ | Low^7 | Yes^2 | No | Shrub | Unk |
| Pedicularis racemosa | No^3 | Yes | Unk | High ³ | Unk | No | Herb | Е |
| Penstemon sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Herb | Unk |
| Phacelia hastata | No^3 | Yes | Low^1 | High ¹ | Unk | Yes | Herb | E |
| Phacelia nemoralis | No^3 | Yes | Unk | Mod. ⁴ | Unk | No | Herb | Unk |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|--|--------------------|-------------------|-------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Phleum pratense | No | No | High ¹ | Low ¹ | Yes ² | Yes | Herb | Е |
| Piperia elegans ssp. elegans | No ³ | Yes | Unk | Mod. ³ | Unk | Yes | Herb | Unk |
| Plantago lanceolata | No^3 | Yes | $High^{16}$ | High ³ | No | Yes | Herb | Unk |
| Poa sp. | No | No | Unk | Mod. | Unk | Yes | Herb | Unk |
| Poa annua | No | No | Low ¹ | Low^1 | No | Yes | Herb | Unk |
| Poa glauca | No | No | Low ¹² | Mod. ¹ | Unk | Yes | Herb | Unk |
| Poa pratensis ssp. pratensis | No | No | High ² | Low ² | Yes ² | Yes | Herb | F |
| Polypodium glycyrrhiza | No | No | Unk | Low ³ | Unk | No | Shrub | L |
| Polystichum munitum | No | No | $Mod.^2$ | Low^1 | Yes^2 | No | Shrub | L |
| Prosartes hookeri var. hookeri | Yes ³ | Yes | Low ¹⁵ | Low ³ | Unk | No | Herb | L |
| Prosartes smithii | Yes^3 | Yes | Low ¹⁵ | Low^3 | Unk | No | Herb | L |
| Prunella vulgaris | No^3 | Yes | Mod. 12 | Mod. ¹ | Unk | Yes | Herb | E |
| Prunus sp. | Yes^3 | Yes | Unk | Unk | Unk | Yes | Shrub | Unk |
| Pseudognaphalium canescens ssp. thermale | No ³ | Yes | Unk | High ³ | Unk | Yes | Herb | E |
| Pteridium aquilinum | No | No | Low^1 | $Mod.^1$ | Yes ² | Yes | Shrub | E |
| Pteridium aquilinum var. pubescens | No | No | Low | Mod. | Yes ² | Yes | Shrub | E |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|---------------------------------------|--------------------|-------------------|--------------------|----------------------|--------------------|------------------|---------|-----------------------------------|
| Pyrola sp. | No ³ | Yes | Unk | Mod. | Unk | Yes | Herb | L |
| Pyrola picta | No^3 | Yes | Low ¹⁵ | Mod. ³ | No^{15} | Yes | Herb | L |
| Ranunculus sp. | No^3 | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Ranunculus occidentalis | No^3 | Yes | Unk | Mod. ³ | Unk | Yes | Herb | Unk |
| Ranunculus uncinatus | No^3 | Yes | Low^1 | Low^1 | No | Yes | Herb | L |
| Ranunculus uncinatus var. parviflorus | No^3 | Yes | Unk | Low ³ | No | Yes | Herb | L |
| Rhododendron macrophyllum | No^3 | Yes | Low ¹ | Low ¹ | Yes ² | No | Shrub | L |
| Ribes sp. | Yes ³ | Yes | Unk | Mod. | Unk | Yes | Shrub | Unk |
| Ribes lobbii | Yes ³ | Yes | Low | Mod. ⁸ | Yes ⁸ | No | Shrub | Unk |
| Ribes sanguineum | Yes ³ | Yes | $High^1$ | Mod. ¹ | Yes ¹ | No | Shrub | E |
| Rosa gymnocarpa | Yes ³ | Yes | High ¹³ | Mod. ¹ | Yes ¹ | No | Shrub | F |
| Rubus sp. | Yes^3 | Yes | Unk | Mod. | Unk | Yes | Shrub | Unk |
| Rubus armeniacus | Yes^3 | Yes | Unk | Mod. ² | Yes ² | Yes | Shrub | E |
| Rubus laciniatus | Yes^3 | Yes | \mathbf{High}^1 | Low ¹ | Yes ¹ | No | Shrub | E |
| Rubus leucodermis | Yes ³ | Yes | $Mod.^1$ | Low^1 | Yes ¹ | Yes | Shrub | Е |
| Rubus nivalis | Yes ³ | Yes | Unk | Low ⁹ | Unk | No | Shrub | L |
| Rubus parviflorus | Yes ³ | Yes | ${\sf High}^1$ | Mod. ¹ | Yes ¹ | Yes | Shrub | E |
| Rubus spectabilis | Yes ³ | Yes | Mod. ¹ | $High^1$ | Yes ¹ | No | Shrub | E |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|-------------------------------------|--------------------|-------------------|-------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Rubus ursinus | Yes ³ | Yes | High ¹ | Mod. ¹ | Yes ¹ | Yes | Shrub | Е |
| Rumex sp. | No^3 | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Rumex acetosa | No^3 | Yes | Unk | Mod. ⁹ | Unk | No | Herb | Unk |
| Rumex acetosella | No^3 | Yes | Unk | Mod. ⁹ | Unk | Yes | Herb | Е |
| Rumex aquaticus var. fenestratus | No ³ | Yes | Unk | Low ⁴ | Unk | No | Herb | Unk |
| Salix sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Shrub | Unk |
| Sambucus sp. | Yes^3 | Yes | Unk | Low | Yes | Yes | Shrub | Unk |
| Sambucus racemosa | Yes^3 | Yes | Mod. | Low | Yes | Yes | Shrub | Е |
| Sambucus racemosa var. racemosa | Yes ³ | Yes | Mod. ¹ | Low ¹ | Yes ¹ | Yes | Shrub | E |
| Sanicula sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Herb | Unk |
| Saxifraga sp. | No^3 | Yes | Unk | Unk | Unk | Yes | Herb | Unk |
| Senecio sp. | No^3 | Yes | Unk | Mod. | Unk | Yes | Herb | Unk |
| Senecio jacobaea | No^3 | Yes | Low^7 | Mod. ³ | Unk | No | Herb | Е |
| Senecio sylvaticus | No^3 | Yes | Unk | High ⁹ | No | No | Herb | Е |
| Solanum dulcamara | Yes^3 | Yes | Low^3 | Mod. ³ | Unk | No | Herb | Unk |
| Sonchus sp. | No^3 | Yes | Unk | Mod. | Unk | Yes | Herb | E |
| Sonchus asper | No^3 | Yes | Unk | Mod. ⁹ | No | Yes | Herb | E |
| Sonchus oleraceus | No^3 | Yes | Unk | Mod. ⁹ | No | Yes | Herb | Unk |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|---|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Sorbus scopulina var. cascadensis | Yes ³ | Yes | Mod. ¹³ | Low | Unk | No | Shrub | Unk |
| Stachys sp. | No^3 | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Stachys mexicana | No^3 | Yes | Unk | Low ³ | Unk | No | Herb | E |
| Stellaria sp. | No^5 | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Stellaria calycantha | No^5 | Yes | Unk | Low^3 | No | Yes | Herb | L |
| Stellaria crispa | No^5 | Yes | Unk | Low ⁸ | Unk | Yes | Herb | Unk |
| Streptopus amplexifolius var. amplexifolius | Yes ³ | Yes | Unk | Low ³ | Unk | No | Herb | L |
| Symphoricarpos albus | Yes ³ | Yes | High ¹ | High ¹ | Yes ¹ | Yes | Shrub | E |
| Symphoricarpos albus var. albus | Yes ³ | Yes | $High^1$ | $High^1$ | Yes | No | Shrub | Е |
| Symphoricarpos hesperius | Yes ³ | Yes | Unk | High ³ | Yes ² | No | Shrub | Unk |
| Synthyris reniformis | No^3 | Yes | Unk | Mod. ³ | Unk | No | Herb | E |
| Taraxacum officinale | No^3 | Yes | Low ¹ | Mod. ¹ | Yes ² | Yes | Herb | Unk |
| Tellima grandiflora | No^3 | Yes | Unk | Low ³ | Unk | No | Herb | E |
| Thalictrum occidentale | No^3 | No | Unk | Low ³ | Unk | No | Herb | Unk |
| Thermopsis sp. | No^3 | Yes ³ | Unk | Mod. | Unk | No | Herb | Unk |
| Thermopsis montana | No^3 | Yes ³ | Unk | Mod. | Unk | No | Herb | E |
| Tiarella trifoliata | No^3 | Yes | High ¹⁶ | Low ³ | Unk | No | Herb | L |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|--|--------------------|-------------------|--------------------|----------------------|------------------|------------------|---------|-----------------------------------|
| Tiarella trifoliata var. laciniata | No ³ | Yes | High ¹⁶ | Low ³ | Unk | No | Herb | L |
| Tiarella trifoliata var. trifoliata | No ³ | Yes | High ¹⁶ | Low ³ | Unk | No | Herb | L |
| Tiarella trifoliata var. unifoliata | No^3 | Yes | High ¹⁶ | Low ³ | Unk | No | Herb | L |
| Tolmiea menziesii | No^3 | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Torilis arvensis | No^3 | Yes | Unk | Mod. ⁸ | No | No | Herb | E |
| Toxicodendron diversilobum | Yes ³ | Yes | Mod. ² | High ¹¹ | Yes ² | Yes | Shrub | F |
| Trichostema lanceolatum | No ³ | Yes | Unk | High ¹ | No | Yes | Herb | Unk |
| Trientalis borealis ssp. latifolia | No^3 | Yes | Unk | Mod. ³ | Unk | No | Herb | L |
| Trifolium sp. | No^3 | Yes ³ | Unk | Low | Unk | Yes | Herb | Unk |
| Trifolium repens | No^3 | Yes ³ | High ¹ | Low ¹ | Unk | Yes | Herb | F |
| Trillium ovatum | No^3 | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Trisetum canescens | No | No | Mod. ¹ | Mod. ¹ | Unk | Yes | Herb | Unk |
| Vaccinium membranaceum | Yes ³ | Yes | Mod. ¹ | Low ¹ | Yes ¹ | No | Shrub | L |
| Vaccinium ovalifolium | Yes ³ | Yes | High ¹ | Mod. ¹ | Yes ¹ | No | Shrub | L |
| Vaccinium ovatum | Yes ³ | Yes | Mod. ¹ | Mod. ¹ | Yes ¹ | No | Shrub | L |
| Vaccinium parvifolium | Yes ³ | Yes | Mod. ¹ | High ¹ | Yes ¹ | No | Shrub | L |

| Accepted Scientific Name | Fleshy- fruited | Insect pollinated | Palatability | Drought Tolerance | Fire tolerant | Heat tolerant | Stratum | Seral Association ^a |
|-----------------------------------|--------------------|-------------------|-------------------|-------------------------|------------------|------------------|---------|-----------------------------------|
| Vancouveria hexandra | No^3 | Yes ³ | Unk | Low ³ | Unk | No | Herb | L |
| Veronica americana | No^3 | Yes | Mod. ¹ | Low^1 | Unk | Yes | Herb | E |
| Veronica officinalis | No^3 | Yes | Unk | $\operatorname{Mod.}^4$ | Unk | No | Herb | E |
| Veronica serpyllifolia | No^3 | Yes | Unk | $Mod.^3$ | Unk | Yes | Herb | Unk |
| Vicia sp. | No^3 | Yes ³ | Unk | High | Unk | Yes | Herb | Unk |
| Vicia americana | No^3 | Yes | $High^1$ | $High^1$ | Yes ² | Yes | Herb | E |
| Vicia americana ssp. americana | No ³ | Yes | High | High | Yes ² | Yes | Herb | F |
| Vicia nigricans ssp. gigantea | No ³ | Yes | Unk | Mod. ³ | Unk | No | Herb | Unk |
| Vicia sativa | No^3 | Yes | $Mod.^1$ | Low^1 | No | Yes | Herb | E |
| Viola sp. | No | Yes | Unk | Low | Unk | Yes | Herb | Unk |
| Viola glabella | No | Yes | Unk | Low^3 | Unk | No | Herb | E |
| Viola palustris | No | Yes | Unk | Low^3 | Unk | No | Herb | Unk |
| Viola sempervirens | No | Yes | Unk | Low^3 | Unk | No | Herb | L |
| Vulpia myuros | No | No | Mod. ¹ | \mathbf{High}^1 | No | Yes | Herb | E |
| Whipplea modesta | No^3 | Yes | Unk | High ³ | Unk | No | Shrub | E |
| Xerophyllum tenax | No^3 | Yes | Low^1 | Mod. ¹ | Yes ² | No | Herb | L |

^a Seral Association: E=early seral, F=facultative, L=late seral and UNK=unknown

Reference Source of species characteristics information.

- USDA, NRCS. 2010. The PLANTS Database (http://plants.usda.gov, 10 August 2010). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- 2 USDA Forest Service Fire Effects Information System (FEIS): http://www.fs.fed.us/database/feis/plants/index.html
- 3 Pojar and Mackinnon Plants of the Pacific Northwest Coast. 1994
- 4 Hitchcock and Cronquist Flora of the Pacific Northwest. 2001
- 5 Woodland, D. W. 1997 Contemporary Plant Systematics
- 6 Cates, R. G. and G. Orians, H. . 1975. Sucessional Status and the Palatability of Plants to Generalized Herbivores. Ecology 56:410-418.
- Range Plants: Their identification, usefulness, and management. Ben Roche 1983
- 8 Gilkey and Dennis Handbook of Northwestern Plants, 2001
- 9 Jepsen Online Interchange California Floristics, University of California, Berkley http://ucjeps.berkeley.edu/interchange/
- Oregon Department of Agriculture, Noxious Weed Control http://www.oregon.gov/ODA/PLANT/WEEDS/
- North American Range Plants 4th Ed. Stubbendieck et al. 1992
- Low C:N ratio are High palatable to browse. Medium C:N medium palatability. High C:N low palatability (USDA Plants Database, 2010)
- 13 Important western browse plants by William Adams Dayton
- 14 Western Regional Climate Center Reno, Nevada
- Key Species for Plant associations on the Rogue River, Siskiyou, and Umpqua National Forests (Compiled by Anita Seda) USDA Forest Service R6-TM-TP-009-89 http://www.reo.gov/ecoshare/publications/documents/SpeciesListTreesShrubs.pdf
- 16 USDA Forest Service Fire Effects Information System (FEIS): http://www.fs.fed.us/database/feis/animals/mammal/ceca/all.html
- 17 Cynosurus Cristatus L. ,Robert W. Lodge, Journal of Ecology. Vol. 47, No. 2 (Jul., 1959), pp. 511-518. Published by: British Ecological Society.
- Department of Primary Industries Victoria Resources Online. http://www.dpi.vic.gov.au/dpi/vro/vrosite.nsf/pages/invasive_holly

APPENDIX C. AIC_c MODELS CONSIDERED

Appendix C. Full set of models assessed using AIC_c and the associated hypotheses. The null model a function of the random effects associated with plot, treatment unit, and site and no fixed effects was included to assess the overall importance the parameters included in the model set.

| Model | Hypothesis Tested |
|---|-------------------|
| Null Model | H-null |
| y = Basal area | H-1 |
| y = Treatment | H-2 |
| y = Treatment + Basal area | H-3 |
| y = Treatment x Basal area | H-3 |
| y = Treatment + Basal area + Slope | H-4 |
| y = Treatment + Basal area + Aspect | H-4 |
| y = Treatment + Basal area + Elevation | H-4 |
| y = Treatment + Basal area + Slope + Aspect | H-4 |
| y = Treatment + Basal area + Slope + Elevation | H-4 |
| y = Treatment + Basal area + Aspect + Elevation | H-4 |
| y = Treatment + Basal area + Slope + Aspect + Elevation | H-4 |
| y = Treatment + Basal area + Slope x Aspect | H-4 |
| y = Treatment + Basal area + Slope x Elevation | H-4 |
| y = Treatment + Basal area + Aspect x Elevation | H-4 |
| y = Treatment x Basal area + Slope | H-4 |
| y = Treatment x Basal area + Aspect | H-4 |
| y = Treatment x Basal area + Elevation | H-4 |
| y = Treatment x Basal area + Slope + Aspect | H-4 |
| y = Treatment x Basal area + Slope + Elevation | H-4 |
| y = Treatment x Basal area + Aspect + Elevation | H-4 |
| y = Treatment x Basal area + Slope x Aspect | H-4 |
| y = Treatment x Basal area $+$ Slope x Elevation | H-4 |
| y = Treatment x Basal area $+$ Aspect x Elevation | H-4 |
| y = Treatment x Basal area + Slope + Aspect + Elevation | H-4 |

APPENDIX D. AIC_c Tables for the best supported models.

Appendix D.1. Parameter estimates of total and functional group cover (%) (n=538). FF=fleshy fruit, IP=insect pollinated, and PB=palatable to browse animals. Only the best approximating models and the null model are presented. When needed, response variables were log(y+1) transformed to satisfy assumptions necessary for regression analysis. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Treat | ment | | • | Model | AICc | ٨ | |
|-----------|---------------------------|-------|-------|--------|-------|-------|-------|---|--------|------------|-------|
| variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | IVIOUEI | AICC | Δ_i | w_i |
| Totala | - | - | - | - | - | - | - | total = 95.49 - 0.650 x liveba | 5037.1 | 0.00 | 0.59 |
| | $\beta_{o\text{-}6}$ Itrt | 96.53 | 94.16 | 105.85 | 94.09 | 92.62 | 99.68 | total = β_{0-6} Itrt - 0.619 x liveba - 0.099 x slope | 5040.6 | 3.58 | 0.10 |
| | - | - | - | - | - | - | - | Null Model ^b | 5096.0 | 58.97 | 0.00 |
| log(FF+1) | $\beta_{o\text{-}6}Itrt$ | 3.44 | 3.36 | 3.84 | 3.72 | 3.70 | 3.75 | $log(FF+1) = \beta_{o-6}Itrt - 0.012 \ x \ liveba - 0.003 \ x \ linasp - 0.0004 \ x \ elev + 0.000004 \ x \ linasp \ x \ elev + 0.0000004 \ x \ linasp \ x \ elev + 0.0000000000000000000000000000000000$ | 1260.8 | 0.00 | 0.40 |
| | β_{o-6} Itrt | 2.77 | 2.73 | 3.23 | 3.09 | 3.07 | 3.12 | $log(FF+1) = \beta_{0-6}Itrt - 0.011 \times liveba - 0.004 \times slope + 0.005 \times linasp$ | 1261.5 | 0.70 | 0.28 |
| | $\beta_{o\text{-}6}Itrt$ | 2.91 | 2.89 | 3.38 | 3.23 | 3.22 | 3.26 | $log(FF+1) = \beta_{o-6}Itrt - 0.011 \ x \ liveba - 0.004 \ x \ slope + 0.005 \ x \ linasp - 0.00009 \ x \ elev$ | 1263.3 | 2.46 | 0.12 |
| | $\beta_{o\text{-}6}Itrt$ | 2.77 | 2.74 | 3.23 | 3.10 | 3.08 | 3.12 | $log(FF+1) = \beta_{o-6}Itrt - 0.011 \ x \ liveba - 0.004 \ x \ slope + 0.008 \ x \ linasp - 0.000003 \ x \ slope \ x \ linasp - 0.0000003 \ x \ slope \ x \ linasp - 0.0000000000000000000000000000000000$ | 1263.6 | 2.79 | 0.10 |
| | $\beta_{o\text{-}6}Itrt$ | 2.66 | 2.62 | 3.12 | 2.97 | 2.99 | 3.02 | $log(FF+1) = \beta_{0-6}Itrt - 0.012 \times liveba + 0.005 \times linasp$ | 1264.6 | 3.75 | 0.06 |
| | - | - | - | - | - | - | - | Null Model ^b | 1321.1 | 60.24 | 0.00 |
| IP^a | β _{o-6} Itrt | 49.36 | 50.50 | 62.71 | 56.09 | 57.51 | 63.49 | $IP = \beta_{o-6}Itrt - 0.295 \text{ x liveba} - 0.104 \text{ x slope} + 0.072 \text{ x linasp}$ | 4813.3 | 0.00 | 0.46 |
| | $\beta_{o\text{-}6}$ Itrt | 52.41 | 53.77 | 65.87 | 59.06 | 60.55 | 66.38 | $IP = \beta_{o-6}Itrt - 0.293 \text{ x liveba} - 0.103 \text{ x slope} + 0.073 \text{x linasp} - 0.002 \text{ x elev}$ | 4815.2 | 1.88 | 0.18 |
| | $\beta_{o\text{-}6}$ Itrt | 50.12 | 51.15 | 63.38 | 56.85 | 58.25 | 64.24 | $IP = \beta_{o-6} Itrt - 0.295 \ x \ liveba - 0.127 \ x \ slope + 0.062 \ x \ linasp + 0.0004 \ x \ slope \ x \ linasp$ | 4815.2 | 1.89 | 0.18 |
| | β_{o-6} Itrt | 46.63 | 47.46 | 59.70 | 53.01 | 55.11 | 60.94 | $IP = \beta_{0-6}Itrt - 0.305 \text{ x liveba} + 0.073 \text{ x linasp}$ | 4816.1 | 2.78 | 0.11 |
| | | | | | | | | Null Model | 4849.3 | 35.99 | 0.00 |
| PB | β _{o-6} Itrt | - | - | - | - | - | - | PB = 46.66 - 0.242 x liveba | 4811.2 | 0.00 | 0.67 |
| | - | - | - | - | - | - | - | Null Model ^b | 4822.9 | 11.67 | 0.00 |

^a Interaction between treatment and basal area is likely due to high leverage of VD100 treatment. Models with the interaction term were excluded from calculation of Δ_i and Akaike weights (w_i).

^b Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.2. Parameter estimates of response type group cover (%) of the fleshy-fruited (FF) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. When needed, response variables were log(y+1) transformed to satisfy assumptions necessary for regression analysis. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | | tment | | | Model | AICc | Δ_i | W i |
|-----------|---|-----------------|-----------------|----------------|----------------|----------------|---------------|--|--------|-----------------------|------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | 110401 | 71100 | <i>□</i> _l | W 1 |
| log(DT+1) | $\beta_{o\text{-}6}Itrt$ | 3.00 | 3.10 | 3.45 | 3.38 | 3.40 | 3.46 | $log(DT+1) = \beta_{o-6}Itrt - 0.008 \ x \ liveba - 0.004 \ x \ linasp - 0.001 \ x \ elev + 0.000003 \ x \ linasp \ x \ elev + 0.0000003 \ x \ linasp \ x \ elev + 0.00000003 \ x \ linasp \ x \ elev + 0.0000000000000000000000000000000000$ | 1259.3 | 0.00 | 0.51 |
| | $\beta_{o\text{-}6}Itrt$ | 2.52 | 2.66 | 3.02 | 2.92 | 2.97 | 3.02 | $log(DT+1) = \beta_{o-6}Itrt - 0.007 \text{ x liveba} + 0.002 \text{ x linasp} - 0.0003 \text{ x elev}$ | 1262.2 | 2.93 | 0.12 |
| | β_{o-6} Itrt | 2.56 | 2.71 | 3.07 | 2.97 | 3.01 | 3.06 | $log(DT+1) = \beta_{o-6}Itrt - 0.007 \ x \ liveba - 0.002 \ x \ slope + 0.002 \ x \ linasp - 0.0003 \ x \ elev$ | 1262.4 | 3.14 | 0.11 |
| | β _{o-6} Itrt β ₇₋₁₂ Itrt | 2.61 -0.0014 | 3.12 -0.0085 | 3.48 -0.009 | 3.04 0.0006 | 3.71 -0.019 | 3.05 0.009 | $log(DT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.004 \ x \ linasp - 0.0006 \ x \ elev - 0.000003 \ x \ linasp \ x \\ elev$ | 1263.2 | 3.95 | 0.07 |
| | - | - | - | - | - | - | - | Null Model ^a | 1284.0 | 24.75 | 0.00 |
| log(FT+1) | β _{o-6} Itrt | 2.73 | 2.70 | 3.23 | 3.10 | 3.08 | 3.11 | $log(FT+1) = \beta_{0-6}Itrt - 0.012 \text{ x liveba} - 0.004 \text{ x slope} + 0.005 \text{ x linasp}$ | 1302.6 | 0.00 | 0.34 |
| | $\beta_{o\text{-}6}Itrt$ | 3.46 | 3.37 | 3.89 | 3.78 | 3.76 | 3.80 | $log(FT+1) = \beta_{o6}Itrt - 0.013 \ x \ liveba - 0.003 \ x \ linasp - 0.0005 \ x \ elev + 0.000005 \ x \ linasp \ x \ elev$ | 1302.9 | 0.32 | 0.29 |
| | $\beta_{o\text{-}6}Itrt$ | 2.92 | 2.90 | 3.43 | 3.28 | 3.27 | 3.29 | $log(FT+1) = \beta_{0-6}Itrt - 0.012 x liveba - 0.004 x slope + 0.005 x linasp - 0.0001 x elev$ | 1304.2 | 1.58 | 0.16 |
| | $\beta_{o\text{-}6}Itrt$ | 2.75 | 2.71 | 3.25 | 3.11 | 3.10 | 3.13 | $log(FT+1) = \beta_{o-6}Itrt - 0.012 \ x \ liveba - 0.005 \ x \ slope + 0.005 \ x \ linasp + 0.000009 \ x \ slope \ x $ linasp | 1304.6 | 2.02 | 0.13 |
| | - | - | - | - | - | - | - | Null Model ^a | 1364.8 | 62.23 | 0.00 |
| log(TT+1) | β _{o-6} Itrt β ₇₋₁₂ Itrt | 1.11 -0.009 | 2.01 -0.02 | 2.64 -0.03 | 2.07 -0.02 | 2.35 -0.02 | 2.60 -0.02 | $log(TT+1) = \beta_{0-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.005 \ x \ s \ lope$ | 1115.0 | 0.00 | 0.28 |
| | β_{o-6} Itrt β_{7-12} Itrt | 1.13 -0.009 | 2.02 -0.02 | 2.66 -0.03 | 2.13 -0.02 | 2.37 -0.02 | 2.61 -0.02 | $log(TT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.008 \ x \ slope - 0.0003 \ x \ linasp + 0.00004 \ x \ slope \ x - 0.000004 \ x \ slope \ x - 0.00004 \ x \ slope \ x - 0.000004 \ x \ slope \ x - 0.00004 \ x \ slope \ $ | 1115.1 | 0.09 | 0.26 |
| | β ₀₋₆ Itrt β ₇₋₁₂ Itrt | 1.02 -0.009 | 1.94 -0.02 | 2.58 -0.03 | 2.03 -0.02 | 2.29 -0.02 | 2.53 -0.02 | $log(TT+1) = \beta_{0-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.005 \ x \ s \ lope + 0.0009 \ x \ linasp$ | 1115.6 | 0.59 | 0.21 |
| | β_{o-6} Itrt β_{7-12} Itrt | 1.14 | 2.05 -0.02 | 2.68 -0.03 | 2.10 | 2.38 -0.02 | 2.63 -0.02 | $log(TT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.005 \ x \ s \ lope - 0.00002 \ x \ elev$ | 1117.1 | 2.02 | 0.10 |
| | β_{0-6} Itrt β_{7-12} Itrt | 1.06 | 1.99 -0.02 | 2.63 -0.03 | 2.07 | 2.33 | 2.57 | $log(TT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.005 \ x \ s \ lope + 0.001 - 0.00002 \ x \ elev$ | 1117.6 | 2.59 | 0.08 |
| | - | - | - | - | - | - | - | Null Model ^a | 1265.3 | 150.29 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.3. Parameter estimates of response type group cover (%) of the insect pollinated (IP) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. When needed, response variables were log(y+1) transformed to satisfy assumptions necessary for regression analysis. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Trea | tment | | | Model | AICc | Λ. | 141 |
|-----------|---------------------------|--------|--------|--------|--------|--------|--------|--|---------|------------|------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | Model | AICC | Δ_i | w i |
| log(DT) | β _{o-6} Itrt | 2.89 | 3.23 | 3.52 | 3.58 | 3.50 | 3.64 | $log(DT) = \beta_{o-6}Itrt - 0.014 \ x \ liveba - 0.004 \ x \ linasp - 0.0005 \ x \ elev + 0.000004 \ x \ linasp \ x \ elev$ | 1386.6 | 0.00 | 0.27 |
| | β_{o-6} Itrt | 2.47 | 2.86 | 3.17 | 3.20 | 3.13 | 3.25 | $log(DT) = \beta_{o-6}Itrt - 0.013 x liveba - 0.004 x slope + 0.002 x linasp - 0.0002 x linasp$ | 1387.2 | 0.66 | 0.19 |
| | $\beta_{o\text{-}6}Itrt$ | 2.09 | 2.46 | 2.77 | 2.83 | 2.75 | 2.89 | $log(DT) = \beta_{o\text{-}6}Itrt - 0.013 \ x \ liveba - 0.004 \ x \ slope + 0.002 \ x \ linasp$ | 1387.3 | 0.71 | 0.19 |
| | $\beta_{o\text{-}6}Itrt$ | 2.14 | 2.51 | 2.82 | 2.89 | 2.81 | 2.95 | $log(DT) = \beta_{o\text{-}6} Itrt - 0.013 \ x \ liveba - 0.005 \ x \ slope + 0.002 \ x \ linasp + 0.00003 \ x \ slope \ x \ linasp$ | 1388.7 | 2.17 | 0.09 |
| | $\beta_{o\text{-}6}Itrt$ | 2.38 | 2.77 | 3.07 | 3.10 | 3.06 | 3.17 | $log(DT) = \beta_{o-6}Itrt - 0.013 \text{ x liveba} + 0.003 \text{ x linasp} - 0.0002 \text{ x elev}$ | 1388.9 | 2.31 | 0.08 |
| | $\beta_{o\text{-}6}$ Itrt | 1.99 | 2.35 | 2.67 | 2.72 | 2.67 | 2.80 | $log(DT) = \beta_{o-6}Itrt - 0.014 x liveba + 0.002 x linas p$ | 1389.0 | 2.43 | 0.08 |
| | - | - | - | - | - | - | - | Null Model ^a | 1433.0 | 46.45 | 0.00 |
| FT | - | - | - | - | - | - | - | FT = 42.07 - 0.173 x liveba | 4823.2 | 0.00 | 0.47 |
| | $\beta_{o\text{-}6}$ Itrt | 55.24 | 56.89 | 61.95 | 52.62 | 51.95 | 58.72 | $FT = \beta_{0-6}Itrt - 0.155 \text{ x liveba} + 0.072 \text{ x slope} - 0.010 \text{ x elev}$ | 4826.5 | 3.38 | 0.09 |
| | $\beta_{o\text{-}6}$ Itrt | 56.56 | 58.38 | 63.44 | 54.18 | 53.02 | 59.92 | $FT = \beta_{0-6}Itrt - 0.149 \text{ x liveba} - 0.010 \text{ x elev}$ | 4826.8 | 3.63 | 0.08 |
| | - | - | - | - | - | - | - | Null Model ^a | 4828.1 | 4.90 | 0.04 |
| log(TT+1) | β_{o-6} Itrt | 1.98 | 2.65 | 3.17 | 2.56 | 2.64 | 2.65 | $log(TT+1) = \beta_{0-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.003 \ x \ slope$ | 1133.7 | 0.00 | 0.17 |
| | β_{7-12} Itrt | -0.020 | -0.020 | -0.036 | | -0.021 | -0.006 | 7 | | | |
| | β _{o-6} Itrt | 2.16 | 2.86 | 3.38 | 2.74 | 2.83 | 2.85 | $log(TT+1) = \beta_{0-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.003 \ x \ s \ lope - 0.0001 \ x \ elev$ | 1134.1 | 0.38 | 0.14 |
| | β_{7-12} Itrt | -0.019 | -0.020 | -0.036 | -0.017 | -0.020 | -0.007 | (a) Foot F 1-12 | | | |
| | β_{o-6} Itrt | 1.90 | 2.56 | 3.09 | 2.47 | 2.56 | 2.56 | $log(TT+1) = \beta_{0-6}Itrt + \beta_{7-12}Itrt x \text{ liveba}$ | 1134.5 | 0.75 | 0.12 |
| | β_{7-12} Itrt | -0.020 | -0.020 | -0.036 | -0.018 | -0.020 | -0.005 | 10g(11-1) p ₀₋₀ mt · p ₁₋₁₂ mt ×m-00u | 113 1.5 | 0.75 | 0.12 |
| | | | | | | | | 9 additional models with $\Delta_i \le 4$, all $w_i < 0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 1287.5 | 153.79 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.4. Parameter estimates of response type group cover (%) of the palatable (PB) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. When needed, response variables were log(y+1) transformed to assumptions necessary for regression analysis. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | Treatment | | | • | Model | A IC- | Δ. | | |
|-----------|---|----------------|----------------|----------------|----------------|----------------|----------------|--|--------|------------|-------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | Model | AICc | Δ_i | w_i |
| log(DT) | β_{o-6} Itrt | 2.89 | 3.23 | 3.52 | 3.58 | 3.50 | 3.64 | $log(DT) = \beta_{o\text{-}6} Itrt - 0.014 \ x \ liveba - 0.004 \ x \ linasp - 0.0005 \ x \ elev + 0.000004 \ x \ linasp \ x \ elev$ | 1386.6 | 0.00 | 0.27 |
| | $\beta_{o\text{-}6}$ Itrt | 2.47 | 2.86 | 3.17 | 3.20 | 3.13 | 3.25 | $log(DT) = \beta_{o\text{-}6}Itrt - 0.013 \text{ x liveba} - 0.004 \text{ x slope} + 0.002 \text{ x linasp} - 0.0002 \text{ x linasp}$ | 1387.2 | 0.66 | 0.19 |
| | $\beta_{o\text{-}6}Itrt$ | 2.09 | 2.46 | 2.77 | 2.83 | 2.75 | 2.89 | $log(DT) = \beta_{o-6}Itrt - 0.013 \text{ x liveba} - 0.004 \text{ x slope} + 0.002 \text{ x linas p}$ | 1387.3 | 0.71 | 0.19 |
| | $\beta_{o\text{-}6}Itrt$ | 2.14 | 2.51 | 2.82 | 2.89 | 2.81 | 2.95 | $log(DT) = \beta_{o-6} Itrt - 0.013 \ x \ liveba - 0.005 \ x \ slope + 0.002 \ x \ linasp + 0.00003 \ x \ slope \ x \ linasp + 0.000003 \ x \ slope \ x \ linasp + 0.0000000000000000000000000000000000$ | 1388.7 | 2.17 | 0.09 |
| | $\beta_{o\text{-}6}Itrt$ | 2.38 | 2.77 | 3.07 | 3.10 | 3.06 | 3.17 | $log(DT) = \beta_{0-6}Itrt - 0.013 x liveba + 0.003 x linasp - 0.0002 x elev$ | 1388.9 | 2.31 | 0.08 |
| | $\beta_{o\text{-}6}$ Itrt | 1.99 | 2.35 | 2.67 | 2.72 | 2.67 | 2.80 | $log(DT) = \beta_{o-6}Itrt - 0.014 \text{ x liveba} + 0.002 \text{ x linas p}$ | 1389.0 | 2.43 | 0.08 |
| | - | - | - | - | - | - | - | Null Model ^a | 1433.0 | 46.45 | 0.00 |
| FT | - | - | - | - | - | - | - | FT = 42.07 - 0.173 x liveba | 4823.2 | 0.00 | 0.47 |
| | β_{o-6} Itrt | 55.24 | 56.89 | 61.95 | 52.62 | 51.95 | 58.72 | $FT = \beta_{0-6}Itrt - 0.155 \text{ x liveba} + 0.072 \text{ x s lope} - 0.010 \text{ x elev}$ | 4826.5 | 3.38 | 0.09 |
| | $\beta_{o\text{-}6}$ Itrt | 56.56 | 58.38 | 63.44 | 54.18 | 53.02 | 59.92 | $FT = \beta_{0-6}$ Itrt - 0.149 x liveba - 0.010 x elev | 4826.8 | 3.63 | 0.08 |
| | - | - | - | - | - | - | - | Null Model ^a | 4828.1 | 4.90 | 0.04 |
| log(TT+1) | β _{o-6} Itrt β ₇₋₁₂ Itrt | 1.98 -0.020 | 2.65 -0.020 | 3.17 -0.036 | 2.56 -0.017 | 2.64 -0.021 | 2.65 -0.006 | $log(TT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.003 \ x \ s \ lope$ | 1133.7 | 0.00 | 0.17 |
| | β_{o-6} Itrt β_{7-12} Itrt | 2.16 -0.019 | 2.86 -0.020 | 3.38 -0.036 | 2.74 -0.017 | 2.83 -0.020 | 2.85 -0.007 | $log(TT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba - 0.003 \ x \ slope - 0.0001 \ x \ elev$ | 1134.1 | 0.38 | 0.14 |
| | β_{o-6} Itrt β_{7-12} Itrt | 1.90 -0.020 | 2.56 -0.020 | 3.09 -0.036 | 2.47 -0.018 | 2.56 -0.020 | 2.56 -0.005 | $log(TT+1) = \beta_{o-6}Itrt + \beta_{7-12}Itrt \ x \ liveba$ | 1134.5 | 0.75 | 0.12 |
| | p _{/-12} tut | 0.020 | 0.020 | 0.050 | 3.010 | 0.020 | 0.005 | 9 additional models with $\Delta_i \le 4$, all $w_i < 0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 1287.5 | 153.79 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.5. Parameter estimates of response type group richness of the fleshy-fruited (FF) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Trea | tment | | | M- 1.1 | A IC- | | |
|----------|---------------------------|------|------|------|-------|-------|-------|--|--------|------------|------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | Model | AICc | Δ_i | w i |
| DT | β_{o-6} Itrt | 4.18 | 4.64 | 4.72 | 4.73 | 5.37 | 4.82 | $DT = \beta_{0-6} Itrt - 0.021 \text{ x liveba} + 0.002 \text{ x linas p}$ | 1751.9 | 0.00 | 0.23 |
| | - | - | - | - | - | - | - | DT = 5.31 - 0.025 x liveba | 1752.2 | 0.27 | 0.20 |
| | $\beta_{o\text{-}6}$ Itrt | 3.85 | 4.28 | 4.38 | 4.41 | 5.04 | 4.51 | $DT = \beta_{o-6}Itrt - 0.021 \text{ x liveba} + 0.002 \text{ x linas } p + 0.0002 \text{ x elev}$ | 1753.5 | 1.62 | 0.10 |
| | | | | | | | | 7 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 1794.6 | 42.73 | 0.00 |
| FT | β _{o-6} Itrt | 6.16 | 6.67 | 6.91 | 6.80 | 7.60 | 6.92 | $FT = \beta_{0-6} Itrt - 0.040 \text{ x liveba}$ | 1975.5 | 0.00 | 0.24 |
| | β_{o-6} Itrt | 5.64 | 6.11 | 6.36 | 6.30 | 7.09 | 6.42 | $FT = \beta_{0-6}Itrt - 0.040 \text{ x liveba} + 0.0003 \text{ x elev}$ | 1976.7 | 1.22 | 0.13 |
| | β_{o-6} Itrt | 6.09 | 6.59 | 6.74 | 6.85 | 7.53 | 6.84 | $FT = \beta_{0-6}Itrt - 0.040 \text{ x liveba} + 0.001 \text{ x linasp}$ | 1977.2 | 1.69 | 0.10 |
| | | | | | | | | 7 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 2057.4 | 81.91 | 0.00 |
| TT | β _{o-6} Itrt | 2.46 | 3.33 | 3.17 | 3.09 | 3.06 | 3.33 | $TT = \beta_{0-6} Itrt - 0.024 \text{ x liveba}$ | 1593.7 | 0.00 | 0.23 |
| | β_{o-6} Itrt | 2.55 | 3.43 | 3.17 | 3.25 | 3.16 | 3.43 | $TT = \beta_{o-6}Itrt - 0.023 \text{ x liveba} - 0.001 \text{ x linasp}$ | 1593.9 | 0.25 | 0.20 |
| | - | - | - | - | - | - | - | TT = 3.21 - 0.028 x liveba | 1595.5 | 1.81 | 0.09 |
| | β_{o-6} Itrt | 2.34 | 3.19 | 3.04 | 2.96 | 2.93 | 3.21 | $TT = \beta_{0-6}Itrt - 0.024 \text{ x liveba} + 0.00008 \text{ x elev}$ | 1595.7 | 2.03 | 0.08 |
| | | | | | | | | 4 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 1656.7 | 63.44 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.6. Parameter estimates of response type group richness of the insect pollinated (IP) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Treat | tment | | | 0 Model | | Δ_i | 141 |
|----------|--|--------|--------|--------|--------|--------|--------|--|--------|------------|------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | | | Δ_i | W i |
| DT | $\beta_{o\text{-}6}Itrt$ | 6.06 | 15.68 | 16.02 | 18.09 | 17.26 | 20.92 | $DT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba}$ | 3004.5 | 0.00 | 0.21 |
| DI | β_{7-12} Itrt | -0.001 | -0.075 | -0.103 | -0.155 | -0.098 | -0.229 | $p_1 - p_{0.6} \text{int} + p_{7-12} \text{int xiive ba}$ | 3004.3 | 0.00 | 0.21 |
| | $\beta_{o\text{-}6}Itrt$ | 6.45 | 16.06 | 16.34 | 18.46 | 17.60 | 21.28 | $DT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba} - 0.013 \text{ x slope}$ | 3004.8 | 0.26 | 0.18 |
| | β_{7-12} Itrt | -0.001 | -0.075 | -0.101 | -0.154 | -0.099 | -0.230 | <i>β</i> ₀₋₆ int + <i>β</i> ₇₋₁₂ int x iiveoa - 0.013 x stope | 3004.0 | 0.20 | 0.10 |
| | β_{o-6} Itrt | 5.06 | 14.62 | 14.96 | 17.10 | 16.26 | 19.98 | $DT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba} + 0.0006 \text{ x elev}$ | 3006.1 | 1.62 | 0.09 |
| | β_{7-12} Itrt | -0.002 | -0.077 | -0.103 | -0.156 | -0.099 | -0.231 | β1 - ρ ₀₋₀ mt · ρ ₇₋₁₂ mt xm·cou · 0.0000 xclev | 5000.1 | 1.02 | 0.07 |
| | β_{o-6} Itrt | 5.31 | 14.87 | 15.14 | 17.34 | 16.47 | 20.22 | $DT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba - 0.013 x slope} + 0.0007 \text{ x elev}$ | 3006.2 | 1.74 | 0.09 |
| | β_{7-12} Itrt | -0.002 | -0.076 | -0.101 | -0.155 | -0.100 | -0.232 | p ₀ -0, 11 + p ₁ -12 11 11 11 11 11 11 11 11 11 11 11 11 1 | 2000.2 | 2., . | 0.05 |
| | 6 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | | | | | 6 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 3091.8 | 87.32 | 0.00 |
| FT | $\beta_{o\text{-}6}Itrt$ | 8.20 | 9.51 | 9.69 | 9.75 | 10.43 | 9.83 | $FT = \beta_{o-6}Itrt - 0.056 \times liveba + 0.0007 \times elev$ | 2330.2 | 0.00 | 0.20 |
| | $\beta_{o\text{-}6}Itrt$ | 9.30 | 10.69 | 10.83 | 10.82 | 11.53 | 10.87 | $FT = \beta_{o-6}Itrt - 0.055 \times liveba$ | 2330.2 | 0.00 | 0.20 |
| | β_{o-6} Itrt | 8.24 | 9.56 | 9.74 | 9.80 | 10.47 | 9.87 | $FT = \beta_{o-6}Itrt - 0.056 \text{ x liveba} - 0.003 \text{ x slope} + 0.0007 \text{ x elev}$ | 2332.1 | 1.92 | 0.08 |
| | | | | | | | | 8 additional models with $\Delta_i \le 4$, all $w_i < 0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 2418.6 | 88.40 | 0.00 |
| TT | β _{o-6} Itrt | 7.37 | 10.90 | 10.42 | 9.89 | 10.17 | 12.01 | $TT = \beta_{0-6}Itrt - 0.097 \text{ x liveba} - 0.014 \text{ x s lope} + 0.001 \text{ x elev}$ | 2800.2 | 0.00 | 0.17 |
| | $\beta_{o\text{-}6}$ Itrt | 9.38 | 13.04 | 12.49 | 11.84 | 12.17 | 13.91 | $TT = \beta_{0-6} Itrt - 0.095 \text{ x liveba} - 0.013 \text{ x s lope}$ | 2801.1 | 0.92 | 0.10 |
| | $\beta_{o\text{-}6}Itrt$ | 7.16 | 10.65 | 10.17 | 9.63 | 10.00 | 11.80 | $TT = \beta_{0-6}Itrt - 0.098 \text{ x liveba} + 0.001 \text{ x elev}$ | 2801.7 | 1.45 | 0.08 |
| | $\beta_{o\text{-}6}Itrt$ | 7.80 | 11.34 | 10.86 | 10.36 | 10.66 | 12.47 | $TT = \beta o - 61 trt - 0.096 x \text{ liveba} - 0.028 x \text{ slope} + .0009 x \text{ elev} + 0.000009 x \text{ slope } x \text{ elev}$ | 2801.7 | 1.48 | 0.08 |
| | | | | | | | | 12 additional models with $\Delta_i \le 4$, all $w_i < 0.07$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 2908.0 | 107.74 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.7. Parameter estimates of response type group richness of the palatable (PB) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. (trt= treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | Treatment Model | | AICc | Δ_i | w i | | | | |
|----------|--|---------------|-----------------|----------------|----------------|----------------|----------------|--|--------|----------------|------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | | | Δ _i | w i |
| DT | β_{o-6} Itrt | 5.75 | 8.01 | 7.96 | 7.67 | 8.55 | 8.20 | $DT = \beta_{o-6} Itrt - 0.025 \ x \ liveba - 0.016 \ x \ slope - 0.001 \ x \ linasp + 0.0001 \ x \ slope \ x \ linasp$ | 2325.9 | 0.00 | 0.09 |
| | β_{o-6} Itrt | 2.52 0.01 | 7.32 -0.031 | 7.60 -0.039 | 7.54 -0.045 | 8.74 -0.057 | 8.95 -0.087 | $DT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \ x \ liveba + 0.003 \ x \ linas p$ | 2326.0 | 0.08 | 0.08 |
| | β_{7-12} Itrt β_{0-6} Itrt β_{7-12} Itrt | 3.05 0.009 | 7.74 -0.030 | 8.01 -0.038 | 8.00 -0.044 | 9.15 -0.056 | 9.33 -0.085 | $DT = \beta_{o\text{-}6}Itrt + \beta_{7\text{-}12}Itrt \ x \ liveba - 0.015 \ x \ slope - 0.0005 \ x \ linasp + 0.0001 \ x \ slope \ x \ linasp$ | 2326.0 | 0.12 | 0.08 |
| | β ₀₋₆ Itrt | 5.48 | 7.97 | 7.69 | 7.38 | 8.34 | | $DT = \beta_{0-6}Itrt - 0.035 \text{ x liveba}$ | 2326.1 | 0.19 | 0.08 |
| | | | | | | | | 16 additional models with $\Delta_i\!\leq\!4,$ all $w_i\!<\!0.07$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 2385.3 | 59.42 | 0.00 |
| FT | β _{o-6} Itrt | 8.94 | 10.28 | 10.65 | 10.20 | 10.92 | 10.57 | $FT = \beta_{0-6} Itrt - 0.059 \text{ x liveba}$ | 2333.7 | 0.00 | 0.09 |
| | β_{o-6} Itrt | 9.11 | 10.49 | 10.80 | 10.38 | 11.12 | 10.78 | $FT = \beta_{o-6}Itrt - 0.057 \times liveba - 0.003 \times linas p$ | 2333.7 | 0.03 | 0.09 |
| | β_{o-6} Itrt | 9.15 | 10.50 | 10.86 | 10.43 | 11.09 | 10.75 | $FT = \beta_{0-6}Itrt - 0.058 \text{ x liveba} - 0.007 \text{ x s lope}$ | 2333.9 | 0.24 | 0.08 |
| | $\beta_{o\text{-}6}$ Itrt | 9.32 | 10.71 | 11.02 | 10.60 | 11.30 | 10.96 | $FT = \beta_{0-6}Itrt - 0.057 \text{ x liveba} - 0.007 \text{ x slope} - 0.003 \text{ x linasp}$ | 2334.0 | 0.27 | 0.08 |
| | | | | | | | | 18 additional models with $\Delta_i \le 4$, all $w_i < 0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 2427.7 | 93.96 | 0.00 |
| TT | β _{o-6} Itrt | 5.05 | 7.16 | 6.72 | 6.45 | 6.63 | 7.10 | $TT = \beta_{0-6}Itrt - 0.044 \text{ x liveba} - 0.008 \text{ x s lope} - 0.004 \text{ x linasp}$ | 2111.6 | 0.00 | 0.28 |
| | β_{o-6} Itrt | 3.76 | 5.93 | 5.50 | 5.19 | 5.48 | 5.89 | $TT = \beta_{o0} Itrt - 0.044 \ x \ liveba + 0.009 \ x \ linasp + 0.0006 \ x \ elev - 0.000007 \ x \ linasp \ x \ elev$ | 2112.8 | 1.13 | 0.16 |
| | β_{o-6} Itrt | 4.84 | 6.93 | 6.49 | 6.22 | 6.45 | 6.90 | $TT = \beta_{0-6}Itrt - 0.044 \times liveba + 0.009 \times linasp$ | 2113.2 | 1.51 | 0.13 |
| | β_{o-6} Itrt | 5.00 | 7.12 | 6.67 | 6.40 | 6.58 | 7.05 | $TT = \beta_{o\text{-}6} Itrt - 0.044 \text{ x liveba} - 0.006 \text{ x s lope} - 0.003 \text{ x linasp} - 0.00002 \text{ slope x linasp}$ | 2113.7 | 2.01 | 0.10 |
| | $\beta_{o\text{-}6}$ Itrt | 4.90 | 7.00 | 6.56 | 6.31 | 6.48 | 6.96 | $TT = \beta_{06} Itrt - 0.044 \ x \ liveba - 0.008 \ x \ s \ lope - 0.004 \ x \ linas p + 0.00009 \ x \ elev$ | 2113.7 | 2.05 | 0.10 |
| | | | | | | | | 2 additional models with $\Delta_i\!\leq\!4,$ all $w_i\!<\!0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 2208.9 | 97.29 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

Appendix D.8. Parameter estimates of response type group evenness of fleshy-fruited (FF) functional group (n=538). DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Trea | tment | | | , 1 , , , | | | |
|----------------------|---|------------------|-----------------|-----------------|-----------------|-----------------|-----------------|---|--------|------------|-------|
| Variable | coefficient | CON | HD | MD | | VD200 | VD100 | Model | AICc | Δ_i | w_i |
| DT | - | - | - | - | - | - | - | ull Model ^a | | 0.00 | 0.67 |
| (n=521) ^b | β _{o-6} Itrt | 0.684 | 0.713 | 0.627 | 0.677 | 0.672 | 0.626 | $DT = \beta_{o-6}Itrt$ | -140.7 | 2.25 | 0.22 |
| FT | β ₀₋₆ Itrt β ₇₋₁₂ Itrt | 0.468 0.004 | 0.807 | 0.701 | 0.676 0.0009 | 0.790 | 0.678 0.001 | FT = β_{0-6} Itrt + β_{7-12} Itrt x liveba - 0.0007 x linasp | -221.5 | 0.00 | 0.18 |
| (n=528) ^b | β_{0-6} Itrt β_{7-12} Itrt | 0.422 0.003 | 0.750 -0.002 | 0.642 | 0.625 0.0008 | 0.738 | 0.623 0.001 | $FT = \beta_{o\text{-}6}Itrt + \beta_{7\text{-}12}Itrt \ x \ liveba - 0.0007 \ x \ linasp + 0.00003 \ x \ elev$ | -221.4 | 0.14 | 0.16 |
| | β_{0-6} Itrt β_{7-12} Itrt | 0.453 0.004 | 0.792 | 0.688 | 0.663 0.0008 | 0.776 -0.003 | 0.663 0.002 | $FT = \beta_{o\text{-}6}Itrt + \beta_{7\text{-}12}Itrt \ x \ liveba + 0.0004 \ x \ slope \text{-} 0.0007 \ x \ linasp$ | | 0.96 | 0.11 |
| | β_{0-6} Itrt β_{7-12} Itrt | 0.405 0.003 | 0.733 -0.002 | 0.627 -0.002 | 0.608 0.0008 | 0.721 | 0.606 0.002 | $FT = \beta_{o\text{-}6} Itrt + \beta_{7\text{-}12} Itrt \ x \ liveba + 0.0005 \ x \ slope - 0.0007 \ x \ linasp + 0.00004 \ x \ elev$ | -220.5 | 1.04 | 0.11 |
| | , | | | | | | | 8 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | -213.9 | 7.66 | 0.00 |
| TT | β _{o-6} Itrt β ₇₋₁₂ Itrt | 0.851 -0.0003 | 0.580 0.003 | 0.599 0.002 | 0.651 0.002 | 0.580 0.002 | 0.628 -0.004 | $TT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \times liveba + 0.002 \times slope - 0.0005 \times linasp$ | 34.2 | 0.00 | 0.30 |
| (n=328) ^b | β_{o-6} Itrt β_{7-12} Itrt | 0.757 0.0003 | 0.530 0.003 | 0.539 0.002 | 0.582 0.001 | 0.526 0.002 | 0.572 | $TT = \beta_{o\text{-}6} Itrt + \beta_{7\text{-}12} Itrt \ x \ liveba + 0.004 \ x \ slope + 0.0003 \ x \ linasp - 0.00002 \ x \ slope \ x \ linasp$ | 34.7 | 0.46 | 0.24 |
| | β_{o-6} Itrt β_{7-12} Itrt | 0.806 -0.0004 | 0.531 0.003 | 0.548 0.002 | 0.605 0.0009 | 0.534 0.002 | 0.586 | $6 	TT = \beta_{1/2} \text{Itrt} + \beta_{2/2} \text{Itrt} \times \text{liveba} + 0.002 \times \text{slone} - 0.0005 \times \text{linasp} + 0.00003 \times \text{elev}$ | | 1.04 | 0.18 |
| | β_{0-6} Itrt β_{7-12} Itrt | 0.790 0.0001 | 0.556 0.002 | 0.564 0.002 | 0.628 0.0007 | 0.549 0.002 | 0.588 | $TT = \beta_{o-6}Itrt + \beta_{7-12}Itrt \times liveba + 0.002 \times slope$ | 35.5 | 1.28 | 0.16 |
| | j- /-12 | | | | | | | 2 additional models with $\Delta_i \le 4$, all $w_i < 0.09$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | 74.9 | 42.70 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

^b Pielou's evenness index was undefined for plots with only one or no species present that contributed to each response type group. Only plots with 2 or more contributing species were included in the model selection process and regression analyses.

Appendix D.9. Parameter estimates of response type group evenness of the insect pollinated (IP) functional group. DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Treat | ment | | | M-1.1 | ATC | | |
|----------------------|---|-------|--------|---------|------------|--------|--------|---|--------|-------|------|
| Variable | ariable coefficient CON HD MD VD300 VD200 VD100 | | Model | AICc | Δ_i | W_i | | | | | |
| DT | - | - | - | - | - | - | - | Null Model ^a | -299.3 | 0.00 | 0.61 |
| (n=536) ^b | - | - | - | - | - | - | - | DT = 0.692 - 0.0004 x liveba | -298.0 | 1.37 | 0.31 |
| FT | β _{o-6} Itrt | 0.397 | 0.750 | 0.676 | 0.728 | 0.788 | 0.691 | $FT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba - } 0.0006 \text{ x linasp}$ | -377.8 | 0.00 | 0.37 |
| 11 | β_{7-12} Itrt | 0.004 | -0.001 | -0.0009 | -0.0003 | -0.003 | 0.0004 | p_{0-6} int + p_{7-12} int x invola = 0.0000 x initas p | -311.0 | 0.00 | 0.57 |
| $(n=535)^{b}$ | $\beta_{o\text{-}6}Itrt$ | 0.388 | 0.739 | 0.668 | 0.718 | 0.778 | 0.680 | $FT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba} + 0.0003 \text{ x slope} - 0.0006 \text{ x linasp}$ | -376.2 | 1.57 | 0.17 |
| | β_{7-12} Itrt | 0.004 | -0.001 | -0.0009 | -0.0004 | -0.003 | 0.0005 | 11 p ₀₋₆ mt + p ₇₋₁₂ mt x n v cou + 0.0000 x stope 0.0000 x masp | 370.2 | 1.57 | 0.17 |
| | $\beta_{o\text{-}6}Itrt$ | 0.385 | 0.733 | 0.659 | 0.713 | 0.773 | 0.675 | $FT = \beta_{0-6}Itrt + \beta_{7-12}Itrt \text{ x liveba - 0.0006 x linas p - 0.00001 x elev}$ | | 1.93 | 0.14 |
| | β_{7-12} Itrt 0.004 - | | -0.001 | -0.0009 | -0.0004 | -0.003 | 0.0004 | 004 1 p ₀₋₀ mt · p ₁₋₁₂ mt x m cod 0.0000 x mmsp 0.00001 x ciev | | 1.75 | 0.14 |
| | $\beta_{o\text{-}6}Itrt$ | 0.368 | 0.727 | 0.654 | 0.702 | 0.765 | 0.667 | $FT = \beta_{o-6} Itrt + \beta_{7-12} Itrt \ x \ liveba + 0.0008 \ x \ slope - 0.0004 \ x \ linasp - 0.000007 \ x \ slope \ x \ linasp$ | -374.9 | 2.89 | 0.09 |
| | β_{7-12} Itrt | 0.004 | -0.001 | -0.001 | -0.0004 | -0.003 | 0.0004 | 11 p ₀₋₆ mit p ₇₋₁₂ mit kinteed to 0.0000 kintepe 0.0000 kintesp 0.00000 kintesp | 371.5 | 2.07 | 0.07 |
| | | | | | | | | 2 additional models with $\Delta_i\!\leq\!4,$ all $w_i\!<\!0.07$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | -363.1 | 14.65 | 0.00 |
| TT | $\beta_{o\text{-}6}Itrt$ | - | - | - | - | - | - | TT = 0.611 + 0.004 x liveba | -254.0 | 0.00 | 0.24 |
| $(n=505)^{b}$ | $\beta_{o\text{-}6}Itrt$ | 0.651 | 0.633 | 0.580 | 0.606 | 0.634 | 0.556 | $TT = \beta_{0-6}Itrt + 0.003 \text{ x liveba} + 0.0007 \text{ x slope}$ | -253.7 | 0.35 | 0.20 |
| | $\beta_{o\text{-}6}Itrt$ | 0.676 | 0.568 | 0.604 | 0.632 | 0.653 | 0.574 | $TT = \beta_{o-6}Itrt + 0.003 \text{ x liveba}$ | -252.2 | 1.86 | 0.10 |
| | β_{o-6} Itrt | 0.671 | 0.656 | 0.598 | 0.625 | 0.657 | 0.579 | $TT = \beta_{0-6}Itrt + 0.003 \text{ x liveba} + 0.0007 \text{ x slope} - 0.0003 \text{ x linasp}$ | -252.0 | 2.03 | 0.09 |
| | | | | | | | | 5 additional models with $\Delta_i\!\leq\!4,$ all $w_i\!<\!0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | -236.3 | 17.78 | 0.00 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

^b Pielou's evenness index was undefined for plots with only one or no species present that contributed to each response type group. Only plots with 2 or more contributing species were included in the model selection process and regression analyses.

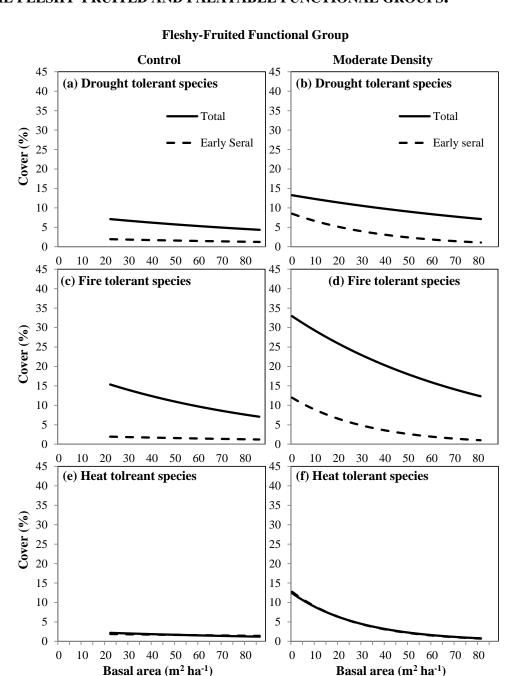
Appendix D.10. Parameter estimates of response type group evenness of the palatable (PB) functional group. DT=drought tolerant, FT=fire tolerant, and TT=heat tolerant. Only the best approximating models and the null model are presented. (trt=treatment, liveba=live conifer basal area, linasp=linearized aspect, elev=elevation).

| Response | Interaction | | | Trea | tment | | | Model | | | |
|---------------|---------------------------|-------|-------|-------|---------|--------|--------|---|--------|------------|-------|
| Variable | coefficient | CON | HD | MD | VD300 | VD200 | VD100 | | | Δ_i | w_i |
| DT | - | - | - | - | - | - | - | Null Model ^a | -237.2 | 0.00 | 0.61 |
| $(n=525)^{b}$ | - | - | - | - | - | - | - | DT = 0.667 + 0.0005 x liveba | -235.6 | 1.53 | 0.28 |
| FT | β _{o-6} Itrt | 0.754 | 0.773 | 0.740 | 0.812 | 0.782 | 0.754 | $FT = \beta_{o\text{-}6} Itrt - 0.002 \ x \ liveba - 0.0006 \ x \ slope + 0.0006 \ x \ linasp - 0.00006 \ x \ elev$ | -424.3 | 0.00 | 0.34 |
| $(n=538)^{b}$ | $\beta_{o\text{-}6}Itrt$ | 0.662 | 0.673 | 0.643 | 0.720 | 0.689 | 0.666 | $FT = \beta_{0-6}Itrt - 0.002 \text{ x liveba} - 0.0007 \text{ x slope} + 0.0006 \text{ x linas p}$ | -423.2 | 1.11 | 0.20 |
| | $\beta_{o\text{-}6}Itrt$ | 0.746 | 0.763 | 0.731 | 0.801 | 0.776 | 0.747 | $FT = \beta_{0-6}Itrt - 0.002 \text{ x liveba} + 0.0006 \text{ x linas p} - 0.00006 \text{ x elev}$ | -423.1 | 1.21 | 0.19 |
| | $\beta_{o\text{-}6}Itrt$ | 0.705 | 0.725 | 0.693 | 0.762 | 0.739 | 0.708 | $FT = \beta_{o\text{-}6} Itrt - 0.002 \ x \ liveba + 0.0001 \ x \ linasp - 0.00004 \ x \ elev - 0.0000003 \ x \ linasp \ x \ elev - 0.0000000000000000000000000000000000$ | -421.8 | 2.53 | 0.10 |
| | $\beta_{o\text{-}6}$ Itrt | 0.643 | 0.653 | 0.624 | 0.700 | 0.673 | 0.649 | $FT = \beta_{o-6}Itrt - 0.002 \text{ x liveba} + 0.0006 \text{ x linas p}$ | | 2.84 | 0.08 |
| | $\beta_{o\text{-}6}Itrt$ | 0.656 | 0.668 | 0.638 | 0.715 | 0.683 | 0.660 | $FT = \beta_{o\text{-}6} Itrt - 0.002 \text{ x liveba} - 0.0005 \text{ x slope} + 0.0006 \text{ x linasp} - 0.000003 \text{ x slope x linasp}$ | | 3.11 | 0.07 |
| | - | - | - | - | - | - | - | Null Model ^a | -404.1 | 20.23 | 0.00 |
| TT | β _{o-6} Itrt | 0.611 | 0.568 | 0.555 | 0.741 | 0.678 | 0.678 | $TT = \beta_{0-6} Itrt + \beta_{7-12} Itrt \times liveba + 0.0009 \times slope$ | -61.9 | 0.00 | 0.21 |
| - 1 1 | β_{7-12} Itrt | 0.003 | 0.004 | 0.003 | -0.0007 | 0.0005 | -0.002 | 71 - p ₀₋₆ me · p ₇₋₁₂ me xiveou · 0.0005 xistope | 01.7 | 0.00 | 0.21 |
| $(n=458)^{b}$ | β_{o-6} Itrt | 0.577 | 0.527 | 0.513 | 0.705 | 0.642 | | $TT = \beta_{0.6} Itrt + \beta_{7.12} Itrt x liveba + 0.0009 x slope + 0.00002 x elev$ | -60.9 | 1.01 | 0.12 |
| | β_{7-12} Itrt | 0.003 | 0.003 | 0.003 | -0.0007 | 0.0004 | -0.002 | p_{0-6} int + p_{7-12} int xiive $ba + 0.0000$ x slope + 0.00002 x elev | | 1.01 | 0.12 |
| | β_{o-6} Itrt | 0.626 | 0.590 | 0.582 | 0.776 | 0.715 | 0.718 | $TT = \beta_{o\text{-}6} Itrt + \beta_{7\text{-}12} Itrt \ x \ liveba - 0.002 \ x \ slope - 0.00002 \ x \ elev + 0.000002 \ x \ slope \ x \ elev$ | | 1.05 | 0.12 |
| | β_{7-12} Itrt | 0.003 | 0.004 | 0.003 | -0.0006 | 0.0006 | -0.002 | | | 1.05 | 0.12 |
| | | | | | | | | 7 additional models with $\Delta_i\!\leq\!4$ including the null model, all $w_i\!<\!0.08$ | | | |
| | - | - | - | - | - | - | - | Null Model ^a | -59.1 | 2.79 | 0.05 |

^a Null model states that the response variable is not a function of overstory density or other parameters considered in model selection, but rather a function of other factors such as spatial correlation associated with plots, treatments and study site locations.

^b Pielou's evenness index was undefined for plots with only one or no species present that contributed to each response type group. Only plots with 2 or more contributing species were included in the model selection process and regression analyses.

APPENDIX E. COVER OF EARLY SERAL AND SHRUB LAYER SPECIES FOR THE FLESHY-FRUITED AND PALATABLE FUNCTIONAL GROUPS.



Appendix E.1 Cover of early seral species and total response type group in the control (a, c and e) and moderate density treatment (b, d and f) along a basal area gradient for the fleshy-fruited functional group.

Palatable Functional Group Control Moderate Density (a) Drought tolerant species (b) Drought tolerant species Total Total Cover (%) Early Seral Early seral 10 20 (c) Fire tolerant species (d) Fire tolerant species Cover (%) 10 20 30 40 50 30 40 (e) Heat tolreant species (f) Heat tolerant species Cover (%) 10 20 30 40 50 60 70 80 10 20 30 40 50 60 70 80

Appendix E.2 Cover of early seral species and total response type group in the control (a, c and e) and moderate density treatment (b, d and f) along a basal area gradient for the palatable functional group.

Basal area (m² ha⁻¹)

Basal area (m² ha⁻¹)