AN ABSTRACT OF THE THESIS OF

Jessica Celis for the degree of Master of Science in Botany and Plant Pathology presented on June 2, 2015.

Title: The Role of Intraspecific Functional Trait Variation in the Differential Decline of Meadow Species Following Conifer Encroachment

Abstract approved: ____
F. Andrew Jones

In the Oregon Cascade Range, conifer encroachment has reduced the extent of mountain meadows by as much as 50% since the mid-1940s. Although encroachment results in a general decline of meadow species abundance and diversity, species differ in their sensitivities to encroachment: some show rapid declines whereas others persist in the understory for many decades. Here, we explore whether this variability can be explained by intraspecific variation in morphological traits associated with the capture of light, the resource assumed to be most limiting in the understory. These include specific leaf area (SLA; ratio of leaf area to mass), allocation of biomass to above- vs. below-ground structures, maximum shoot height, and clonality. We hypothesized that sensitivity to encroachment is greater in non-clonal species and in those that show less variation in trait expression across the light gradient. From a larger set of meadow species at Bunchgrass Ridge, Oregon, we chose 13 (10 forbs and three grasses) that varied in their rates of decline across a chronosequence of encroachment states. For each species we estimated cover and light availability at multiple locations representing the encroachment gradient (open meadow to >100-year-old forest). We modeled the relationship between cover and light and computed an index of sensitivity to encroachment, SEI, as the coefficient of

variation (CV) of predicted cover across the range of light values. We then measured the morphological traits of 15-17 mature individuals of each species in locations representing the range of light environments. For each species, variation in a trait (trait variability) was expressed by the linear slope of the relationship with light. Clonality was treated as an ordinal variable with one of three value, 0 (non-clonal), 0.5 (limited clonality), or 1 (strongly clonal). To test the hypothesized relationship between sensitivity to encroachment and trait variability, we computed for each trait, the correlation between SEI and trait variability ($n = 13$).

Clonality and intraspecific trait variability explained little variation in SEI. Although SLA increased in the shade for all meadow species (an adaptive response to shade) the magnitude of response (slope of SLA-light relationship) did not correlate with sensitivity to encroachment ($r = 0.24$, $p = 0.46$). Analyses of the components of SLA revealed a significant correlation with SEI for leaf area, but not leaf mass. Leaf area increased in the shade for less sensitive species, but declined in the shade for more sensitive species. The adaptive significance of this pattern is not clear given that leaf area and plant cover (upon which SEI is based) likely co-vary. Sensitivity to conifer encroachment may relate more to variation in the physiological traits of species (e.g., adjustment of photosynthetic systems) or in the ability of species to respond to changes in resources or limiting factors other than light.

The Role of Intraspecific Functional Trait Variation in the Differential Decline of Meadow Species Following Conifer Encroachment

by
Jessica Celis

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented June 2, 2015
Commencement June 2015

Master of Science thesis of Jessica Celis presented on June 2 2015.

APPROVED:

Major Professor, representing Botany and Plant Pathology

Head of the Department of Botany and Plant Pathology

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jessica Celis, Author

ACKNOWLEDGEMENTS

I want to express my sincere appreciation to those who helped me to complete this project and accomplish a major goal in my life. First, I would like to thank my major advisor, Andy Jones, who supported me in conducting research in a field that has captured and held my interest for years. In addition, Andy Jones provided R-support, data analysis guidance, and read many iterations of this thesis to help improve its readability and consistency. I would also like to thank my co-advisor, Charlie Halpern, whose input and support on the experimental design, data collection, data analysis, and writing of this project were invaluable. Joe Antos also provided valuable input in the design of this project. Bruce McCune provided invaluable statistical advice. Ariel Muldoon also provided critical statistical and R-programming support as I worked through my analyses. My committee member, Julia Jones, encouraged me to meet with my prospective advisor and others in the Botany and Plant Pathology Department—advise that was critical to my acceptance into the Master's program. Mark Schulze, Director of the H.J. Andrews Experimental Forest (HJA), has been a wonderful boss and mentor over the four years that I have worked at HJA, providing logistical support and advice during my field season. I would not have been able to collect these data without my field and lab assistant, Katherine Dymek. My husband, Chris Parson, also helped with data collection and provided unwavering love and encouragement as I took the steps needed to complete this project. I want to acknowledge the love and support that I also received from my family and friends. Specifically, my brother, Shane Celis, was instrumental in helping me learn R-programming and spent many hours patiently working with me to solve the programming problems that I faced with data analyses and figure production. My good friend, Ari DeMarco, also took the time to read and edit my thesis. I would also like to thank all of the members of the Jones Lab who took time to read and offer feedback on my thesis. Last, but not least, I would like to thank the organizations and institutions that provided funding for my Master's project. Thank you to the Department of Botany and Plant Pathology for offering me a teaching assistantship during my first 3 terms as a Master's student. It was not only a job, but also a learning and growing experience. I also want to thank the HJA LTER Program for RA funding during the last year of my Master's program and for supporting the statistical consulting provided by Ariel Muldoon. Finally, I want to thank the Portland Garden Club Katherine Pamplin Scholarship, and Moldenke Scholarship for funding that covered field expenses and travel.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

Table Page

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLE

CHAPTER 1 General Introduction

This work has been inspired by the unique beauty of the meadows and grasslands of the Pacific Northwest and their potential loss to conifer encroachment. Coniferous forests cover most of the Western Cascade Range (Hickman 1976); meadows occupy only 5% of the landscape. The low-growing forbs, grasses, and sedges that dominate these meadows contribute as much as 85% of the plant biodiversity of this region (Hickman 1976). In the spring, forbs carpet the ground with vibrant colors. These wildflower displays attract a wide variety of pollinators including flies, moths, butterflies, bees, beetles and humming birds (Pfeiffer 2012, Highland and Jones 2014). In addition, meadows provide habitat for ground-nesting birds and small mammals like gophers, and are foraging or hunting grounds for larger wildlife including deer, bears, coyotes, and mountain lions.

Encroachment of grasslands by woody plants is occurring around the world (Archer et al. 1995, Scholes and Archer 1997, Briggs et al. 2005): Australia (Brown and Carter 1998), Africa (Moleele and Perkins 1998, Belay et al. 2013), Europe (Waesch and Becker 2009), North America (Archer et al. 1995, Highland and Jones 2014), and South America (Dussart et al. 1998). Multiple sources of evidence in the Pacific Northwest indicate that montane meadows have contracted by as much as 50% since the mid-1940s (Dailey 2007, Takaoka and Swanson 2008, Zald 2009). As trees establish in open areas they shade out meadow species and facilitate recruitment of forest understory species; with sufficient time, forest species come to dominate former meadows (Haugo and Halpern 2007). Multiple explanations for this phenomenon have been proposed, including cessation of sheep grazing, long-term suppression of fire, changes in climate, and positive interactions among trees that promote the continued establishment of tree seedlings (Vale 1981, Miller and Halpern 1998, Halpern et al. 2010, Rice et al. 2012).

A chronosequence-based study of meadow loss in the Oregon Cascades demonstrates that meadow species differ in their responses to encroachment (Haugo and Halpern 2007). Whereas some species are eliminated quickly, others persist in low abundance for many decades. Conifer encroachment of meadows thus contributes to an extinction debt, whereby loss of meadow species lags behind more immediate changes in habitat quality (Tilman et al. 1994, Highland and Jones 2014). Differences in extinction rate often vary with the life history traits of species, including longevity. For example, as habitat conditions change, short-lived annuals—dependent on recruitment from seed—may decline more quickly than longer-lived perennials that can tap carbohydrate reserves in root systems, at least in the short term (Schleuning and Matthies 2008). Here we explore whether variation in the functional traits of species—specifically those related to the capture of light—contribute to this variation in survival.

Functional traits are those that influence species' survival or reproduction (Reich et al. 2013). Trait-based ecology posits that environmental filtering is a major driver of community assembly; species with similar functional traits are more likely to be present under particular environmental conditions than others (Ackerly and Cornwall 2007, Cingolani et al. 2007, Jung et al. 2010). However, in many functional trait studies, trait variation within species is not treated as variable across environmental gradients (Ackerly and Cornwell 2007). Instead, trait studies often use the mean field approach (Ackerly and Cornwell 2007, Hulshof and Swenson 2010, Jung et al. 2010, Messier et al. 2010, Harrison et al. 2010, Castro-Diez 2012), where the mean value for a given species' trait is assigned to each species. Alternatively, other approaches have assigned species to discrete functional groups based upon clustering analyses (Silverton et al. 1993, Petchey et al. 2006, Ikuaniece et al. 2013). These types of studies have provided a novel perspective into understanding how environmental filtering may be involved in determining the niche breadth of species and community assembly patterns. For example, Cingolani et al. (2007) examined how resource acquisition traits of 57 grass species changed over different grazing intensities and a water availability gradient to better understand which traits, if any, were being filtered by these two variables. They found that traits related to plant size (height, leaf area, leaf thickness) were correlated with increased grazing intensity and that traits related to photosynthesis (SLA and leaf toughness) were related to increased water stress. While results from these trait-based approaches are valuable, the analytical methods applied ignore intraspecific trait variation and assume that the mean of the trait and environmental variables throughout the range of a species occurrence is indicative of species performance optimum (Castro-Diez 2012).

The body of work that seeks to explain intraspecific trait variation of a community to changes along an environmental gradient is shallow compared to studies that look at trait variation among species. Intraspecific trait variation studies have allowed ecologists to answer questions relating to the tolerance levels and niche breadth of species across environmental gradients (McAlpine and Jesson 2007, Suding et al. 2008, Jung et al. 2010, Hulshof and Swenson 2010, Swenson 2013, Gianoli and Saldana 2013). The degree to which species can adjust their SLA and leaf size has been correlated with their ability to tolerate shaded environments, where shade tolerant species have a greater ability to adjust their leaf traits than shade intolerant species (Gianoli and Saldana 2013). McConnaughay and Coleman (1999) observed that herbaceous annuals shifted allocation from shoots to roots when grown in shaded environments as opposed to high light ones. They found that three herbaceous annual species responded to light availability by altering allocation of biomass to below ground structures in high light environments; consistent with optimal resource partitioning theory (e.g., plants tend to allocate biomass to the organ acquiring the most limited resource). In another example, Burns (2004) examined the patterns of SLA to the structure of a temperate heath community on a gradient between peat bogs and the understory of coniferous forests in British Columbia. He found that increases in intraspecific variation in SLA seemed to increase the niche breadth of species across this gradient. Studies like these illustrate the value of examining intraspecific trait variation when examining patterns of species abundance and community assembly along an environmental gradient.

I conducted a study to explore how the morphological traits of meadow species change along an encroachment gradient defined by declining levels of understory light. My objective was to determine whether differences in species' sensitivities to encroachment (i.e., differing rates of decline) could be explained by differences in variability across the encroachment gradient for traits directly or indirectly related to the capture of light. These traits included specific leaf area (SLA, ration of leaf area to mass), allocation to above- vs. below-ground structures, shoot height, and degree of clonality (the ability to grow laterally). I hypothesized that species that are more sensitive to encroachment would show less variation in trait expression across the light gradient compared to species that are less sensitive to encroachment. Additionally, I hypothesized that light would act as an environmental filter on the functional composition of residual meadow communities such that shaded areas would have a greater relative abundance of species that are more variable in their traits and have greater clonal potential.

LITERATURE CITED

Ackerly, D.D., and Cornwell, W. (2007). A trait based approach to community assembly: partitioning of species trait values into within- among-community components. *Ecology*

Letters, **10**, 135-145.

Archer, S., Schimel, D.S., and Holland, E.A. (1995). Mechanisms of shrubland expansion: land use, climate or CO_2? *Climate Change,* **29**, 91-99.

Baley, T. A., Totland, O., and Moe, S.R. (2013). Ecosystem responses to woody plant encroachment in a semiarid savanna rangeland. *Plant Ecology* **214**: 1211-1222.

Blom, C.W.P.M., Voesenek, L.A.C.J. (1996). Flooding: the survival strategies of plants. *Trees* **11**: 290-295.

Briggs, J.M., Knapp, A., Blair, J., Heisler, J., Hoch, G., Lett, M., and McCarron, J. (2005). An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic Grassland to Shrubland. *BioScience*, **55**, 243-254.

Brown, Joel R. and Carter, J. (1998). Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**:93-102.

Burns, K.C., 2004. Patterns in specific leaf area and the structure of a temperate heath community. *Diversity and Distributions* **10**:105-112.

Castro-Diez, P. (2012). Functional trait analyses: Scaling up from species to community level. *Plant Soil* **357**: 9-12.

Cingolani A.M. Cabido, M., Gurvich, D.E., Renison, D., and Diaz, S., 2007. Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? *Journal of Vegetation Science* **18**: 911-920.

Dailey, M.M. (2007). Meadow Classification in the Willamette National Forest and Conifer Encroachment Patterns in the Chucksney-Grasshopper Meadow Complex, Western Cascade Range, Oregon. (Master's Thesis). Retrieved from Oregon State Student Archives.

Dussart, E., Lerner, P., and Peinetti, R. (1998). Long-term dynamics of two populations of Prosopis Caldenia Burkart. *Journal of Range Management* **51**: 685-691.

Gianoli, E., and Saldana, A. (2013). Phenotypic selection on leaf functional traits of two congeneric species in a temperate rainforest is consistent with their shade tolerance. *Oecologia* **173**: 13-21.

Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K., Ni, J., and Sutra, J.P. (2010). Ecophysiological and bioclimatic foundations for global plant functional classification. *Journal of Vegetation Science* **21**: 300-317.

Haugo, R. D., and Halpern, C. B. (2007). Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Botany* **88**: 285-298.

Hickman, J.C. (1976). Non-forest vegetation of the western Cascade Mountains of Oregon. *Northwest Science* **50**: 145-155.

Highland, S. and Jones, J. (2014). Extinction debt in naturally contracting mountain meadows in the Pacific Northwest, USA: varying response of plants and feeding guilds of nocturnal moths. *Biodiversity Conservation* **23**: 2529-2544.

Hulshof, C.M. and Swenson, N.G. (2010). Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology* **24**: 217-223.

Ikuaniece, S., Brumelis, G., Kasparinskis, R., Nikodemus, O., Straupe, I., and Straupe, J. (2013). Effects of soil and canopy factors on vegetation of *Quercus robur* woodland in the boreo-nemoral zone: a plant-trait based approach. *Forest Ecology and Management* **295**: 43-50.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**: 1134-1140.

Kroon, H.D. and Hutchings, M.J. (1995). Morphological plasticity in clonal plants: the foraging concept reconsidered. *Journal of Ecology* **83**: 143-152.

McAlpine, K.G. and Jesson, L.K. (2007). Biomass allocation, shade tolerance and seedling survival of the invasive species *Berberis darwinii* (Darwin's barberry). *New Zealand Journal of Ecology* **31**: 1-12.

McConnaughay, K.D.M., and Coleman, J.S. (1999). Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* **80**: 2581-2593.

Messier, J., McGill, B.J., and Lechowicz, M.J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838-848.

Miller, E.A., and Halpern, C.B. (1998). Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetative Science* **9**: 265–282.

Moleele, N.M. and Perkins, J.S. (1998). Encroaching woody plant species and boreholes: is cattle density he main driving factor in the Oilfants Drift communal grazing land, south-eastern Botswana. *Journal of Arid Environments* **40**:245-253.

Osnas, L.D., Lichstein, J.W., Reich, P.B. and Pacala, S.W. (2013). Global leaf trait relationships: mass, area, and the leaf economic spectrum. *Science* **130**: 741-744.

Pfeiffer, Vera (2012). Influence of spatial and temporal factors on plants, pollinators, and plant-pollinator interactions in montane meadows of the western cascades. M.S. Thesis. Scholar's Archives. Oregon State University, Corvallis.

Petchey, O.L. and Gaston, K. (2006). Functional diversity: back to basics and looking forward. *Ecological letters* **9**: 741-758.

Reich, P., Walters, M., and Ellsworth, D. (1997). From tropics to tundra: Global convergence in plant functioning. *Ecology* **94**: 13730-13734.

Rice, J., Halpern, C., Antos, J., and Jones, J., (2012). Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow. *Plant Ecology* **213**: 555-568.

Schleuning, M. and Matthies, D. (2008). Habitat change and plant demography: assessing the extinction risk of a formerly common grassland perennial. *Conservation Biology* **23**: 174-183.

Silvertown J., Franco, M., Pisanty, I., and Mendoza, A. (2014). Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *British Ecological Society* **81**: 465-476.

Soudzilovskaia, N., Elumeeva, T., Onipchenko, V., Shidakov, I., Salpagarova, F., Khubiev, A., Tekeev, D., and Cornelissen, J. (2013). Functional traits predict relationship between abundance dynamic and long-term climate warming. *PNAS* **110**: 18180-1814.

Suding, K., Lavorel, S., Chapin III, F.S., Cornelissens, J., Diaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S., and Navas, M.L. (2008). Scaling environmental change through the community level: a trait based response-and-effect framework for plants. *Global Change Biology* **14**: 1125-1140.

Svensson, B., Floderus, B., and Callaghan, T. (1994). *Lycopodium annotinum* and light quality: growth responses under canopies of two *Vaccinium* species. *Folia Geobotanica and Phytotaxinomica* **29**: 159-166.

Takaoka, S., and Swanson, F.J. (2008). Change in extent of meadows and shrub fields in the central western Cascade Range, Oregon. Prof. Geogr. **60**: 527-540.

Tilman D., May, R. M., Lehman, C. L., and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature* **371**: 65-66.

Vale, T.R. (1981). Tree invasion of montane meadows in Oregon. *American Midland Naturalist* **105**: 61–125.

Waesch, G., and Becker T. (2009). Plant diversity differs between young and old mesic meadows in a central European low mountain region. *Agriculture, Ecosystems, and Environment* **129**: 457-464.

Zald, H.S.J. (2009). Extent and spatial patterns of grass bald land cover change (1948-2000), Oregon Coast Range, USA. *Plant Ecology* **201**:517-529.

CHAPTER 2

The role of intraspecific functional trait variation in determining the differential decline of meadow species following conifer encroachment

Jessica Celis, Charles B. Halpern, and F. Andrew Jones

In preparation for journal submission

ABSTRACT

In the Oregon Cascade Range, conifer encroachment has reduced the extent of mountain meadows by as much as 50% since the mid-1940s. Although encroachment results in a general decline of meadow species abundance and diversity, species differ in their sensitivities to encroachment: some show rapid declines whereas others persist in the understory for many decades. Here, we explore whether this variability can be explained by intraspecific variation in morphological traits associated with the capture of light, the resource assumed to be most limiting in the understory. These include specific leaf area (SLA; ratio of leaf area to mass), allocation of biomass to above- vs. below-ground structures, maximum shoot height, and clonality. We hypothesized that sensitivity to encroachment is greater in non-clonal species and in those that show less variation in trait expression across the light gradient. From a larger set of meadow species at Bunchgrass Ridge, Oregon, we chose 13 (10 forbs and three grasses) that varied in their rates of decline across a chronosequence of encroachment states. For each species we estimated cover and light availability at multiple locations representing the encroachment gradient (open meadow to >100-year-old forest). We modeled the relationship between cover and light and computed an index of sensitivity to encroachment, SEI, as the coefficient of variation (CV) of predicted cover across the range of light values. We then measured the morphological traits of 15-17 mature individuals of each species in locations representing the range of light environments. For each species, variation in a trait (trait variability) was expressed by the linear slope of the relationship with light. Clonality was treated as an ordinal variable with one of three value, 0 (non-clonal), 0.5 (limited clonality), or 1 (strongly clonal). To test the hypothesized relationship between sensitivity to encroachment and trait variability, we computed for each trait, the correlation between SEI and trait variability ($n = 13$).

Clonality and intraspecific trait variability explained little variation in SEI. Although SLA increased in the shade for all meadow species (an adaptive response to shade) the magnitude of response (slope of SLA-light relationship) did not correlate with sensitivity to encroachment ($r = 0.24$, $p = 0.46$). Analyses of the components of SLA revealed a significant correlation with SEI for leaf area, but not leaf mass. Leaf area increased in the shade for less sensitive species, but declined in the shade for more sensitive species. The adaptive significance of this pattern is not clear given that leaf area and plant cover (upon which SEI is based) likely co-vary. Sensitivity to conifer encroachment may relate more to variation in the physiological traits of species (e.g., adjustment of photosynthetic systems) or in the ability of species to respond to changes in resources or limiting factors other than light.

INTRODUCTION

Encroachment of grasslands by woody plants is occurring globally (Archer et al. 1995, Schole and Archer 1997, Briggs et al. 2005, Highland and Jones 2014). In parts of the western Cascade and Coast Ranges of Oregon, conifer encroachment has reduced the extent of mountain meadows by as much as 50% since the mid-1940s (Dailey 2007, Takaoka and Swanson 2008, Zald 2009). Many factors have contributed to the accelerated pace of meadow loss in this region, including cessation of sheep grazing, long-term suppression of fire, changes in climate, and strong positive interactions among invading trees (Vale 1981, Miller and Halpern 1998, Rice et al. 2012). Although species loss is a natural consequence of encroachment, meadow forbs and grasses show surprising variation in the pace at which they are eliminated. Some species show rapid declines once trees establish; others persist in the understory for many decades (Haugo and Halpern 2007). Here, we explore whether these differences in survival can be explained by intraspecific variation in species' functional traits (specific leaf area [SLA; fresh leaf area:dry mass ratio], allocation to above- vs. below-ground structures, maximum shoot height, and clonality) under the assumption that greater intraspecific variation in these resource acquiring traits enables a species to occupy a broader range of environmental niches.

Knowledge of plant functional traits is fundamental to our understanding of species' distributions in space and time (Reich et al. 1997, Ackerly and Cornwell 2007, Cingolani et al. 2007, Osnas et al. 2013). That said, in many studies of species' environmental or temporal distributions, traits are typically assumed to vary only among species (Silverton et al. 1993, Petchey et al 2006, Cornwell and Ackerly 2009, Hulshof and Swenson 2010, Messier et al. 2010, Harrison et al. 2010, Castro-Diez 2012, Ikuaniece et al. 2013), rather than within them (Laurens et al. 2012, Violle et al. 2012, Gianoli and Saldana 2013). Nevertheless, knowledge of intraspecific trait variation has been useful in explaining species' environmental tolerances and niche breadths (McAlpine and Jesson 2007, Suding et al. 2008, Jung et al. 2010, Hulsof and Swenson 2010, Gianoli et al. 2012, Gianoli and Saldana 2013). For example, an increase in SLA is a common response to shading because it facilitates greater capture of light for a given investment in leaves (Ackerly and Cornwell 2007). The ability to adjust SLA and leaf size is correlated with species shade tolerance in Chilean tropical forests (Saldana et al. 2005, Gianoli and Saldana 2013). Similarly, intraspecific variation in SLA correlates with the niche breadth of heathland species across a light gradient from open peat bog to closed coniferous forest (Burns 2004).

Plants can also adjust allocation of biomass in response to changes in resource availability. Optimal partitioning theory (OPT) predicts that plants should allocate biomass to the organ that acquires the most limiting resource (Bloom et al. 1985, Poorter 2011). Consistent with

OPT, McConnaughay and Coleman (1999) observed that herbaceous annuals shifted allocation from shoots to roots when grown in shaded environments as opposed to high light ones. Plasticity can also be expressed through changes in plant form that are advantageous to resource capture. For example, species may vary in their abilities to etiolate (elongate stems in the shade) thus escaping light interception by neighboring species (Hirose and Werger 1995). Finally, species vary in their clonal potential which increases the ability to spread laterally via rhizomes, stolons, or tillers and capitalize on local variation in resource availability (van Groenendael and de Kroon 1990, Kroon and Hutchings 1995, Stueffer et al. 1996, Humphrey and Pyke 1997, Louapre et al. 2012, Hendriks et al. 2015). Plants in resource-rich environments tend to develop short internodes between ramets whereas plants in resource-limited environments (e.g., low light) tend to develop longer internodes, and increase their capacity for light capture (Dong 1992, Svensson et al. 1994).

In this study, we explore whether the differential decline in abundance, or sensitivity, of meadow species to encroachment can be explained by intraspecific variation in morphological traits related to light capture because light is the resource assumed to be most limiting in the understory (Gleeson and Tilman 1992). We hypothesize that sensitivity is greater in species that are non-clonal and show less variability in trait expression across the light gradient (*H1*). By extension, we hypothesize that encroachment (via light reduction) acts as a filter on the functional composition of species, reducing the relative abundance of those with limited morphological variability (*H2*). Although we are unable to infer the mechanistic bases of this variation (e.g., phenotypic plasticity vs. genetic variability), we can explore whether it appears adaptive and consistent with species' sensitivities to light.

METHODS

Study site

Bunchgrass Ridge is located on the western slope of the High Cascade Range in the Willamette National Forest of Oregon (~1350 m elevation: 44°17'N, 121°57'W) (Appendix Fig. A1). The climate is characterized by cool, wet winters and warm, dry summers. Temperatures at Santiam Pass, 17 km to the north of Bunchgrass Ridge, average -3.1°C in January and 60°C in July. Annual precipitation is ~216 cm, but it is highly seasonal (7.5% falls between June and August). Total snowfall averages ~11 m and results in a deep snowpack that can persist until late May or early July (Western Regional Climate Center 2011).

The 100-ha plateau supports a mosaic of open meadows and coniferous forests of varying age, reflecting two centuries of invasion of *Abies grandis* and *Pinus contorta* (Haugo and Halpern 2010, Rice et al. 2012). Meadows support a diversity of graminoids and forbs characteristic of mesic and dry-site meadows of this region (Haugo and Halpern 2007, Halpern et al. 2012, McCain et al. 2014). Forests understories contain a mix of residual meadow species and forest herbs whose relative abundance and diversity vary with the age and density of trees (Haugo and Halpern 2007). Soils are fine sandy loams derived from andesitic basalts and tephra deposits with varying amounts of glacial derived stones and boulders (http://depts.washington.edu/bgridge/J.PDFs/Bunchgrass_Ridge_pedons.pdf). Soil profiles from both open meadow and closed-forest communities indicate that meadow vegetation had dominated the plateau for centuries prior to recent tree invasions (Haugo and Halpern 2007). Mountainous areas tend to shift where meadows occur, such that there is a cycling in the landscape between forested areas and meadows (Archer et al. 1995). Why Bunchgrass Ridge became a meadow and has supported meadows for as long as it has remains an unanswered question.

Measurements of meadow species cover and light

We combined two sets of data to quantify the relationships between meadow species cover and light availability. The first set, collected in 2004, include those used by Haugo and Halpern (2007) to explore relationships between forest age structure, light, and species' abundance. Cover (%) of individual meadow species was visually estimated in 537, 10 m^2 subplots representing the range of encroachment states including uninvaded meadow to old forest (19th-century encroachment). Each subplot was sampled with a diagonally laid transect (north-west to south-east corner) consisting of four 1 x 1 m quadrats spaced 1 m apart (Appendix Fig. A2); cover was then averaged for the four quadrats. A hemispherical photograph was taken ~1.3 m from the ground surface at the transect midpoint from which total transmitted light (% of above-canopy light) was estimated over the growing season (e.g. April to September) using Gap Light Analyzer software (Frazier et al. 1999). The second set of data, collected in 2014, is from a companion study of flower production in meadow forbs (Celis et al. unpublished ms). In total, 80 subplots were sampled across the encroachment gradient, as described above, but our sampling included greater representation of open-meadow (higher-light) environments than the 2004 dataset. Cover was estimated as in 2004, but hemispherical photographs were taken above each of the four quadrats at 0.7 m from the ground surface; cover and % transmittance values were then averaged for the four quadrats.

Species selection

From the approximately 70 meadow species that have be found at Bunchgrass Ridge, we chose 13 (10 forb and three grass species, Table 2.1) that represented a range of the rate in which species' abundance declines (Haugo and Halpern 2007). Nomenclature follows USDA Plants (2015). For each species, we chose 15-17 mature individuals (N = 216) for destructive sampling using a stratified-random approach to ensure full representation of the light and encroachment gradient. Specifically, 3-5 mature, healthy individuals were chosen from existing or newly established subplots within each of four general light environments: large open meadows distant from forest edge; smaller residual meadow openings; young, more open forests; and older, closed-canopy forests. A hemispherical photograph was taken above each individual to quantify light availability following Haugo and Halpern (2007).

Trait measurements

Plants were excavated between 25 June and 5 August 2014. From the initial shoot, all connected shoots and components of the root system (roots, rhizomes, bulbs, or other storage organs) were carefully extracted using small hand tools and fingers (Antos and Zobel 1984, Lezberg et al. 1999). Maximum shoot height (hereafter, shoot height) was measured as the distance from the ground surface to the tip of tallest leaf. For each plant, shoots, leaves, reproductive tissues, and root systems were bagged separately and transported to the lab. Root systems were carefully washed to remove all soil. All plant components were dried at 86°C for 48 hours or until weights stabilized. Leaf traits (fresh leaf area, dry leaf mass, and SLA) were measured for 1-5 healthy, mature leaves; they were pressed and photographed in the field, prior to drying. Leaf area was estimated using ImageJ 1.48v software (Rasband 2014). Leaf values were averaged for each individual. The ratio of above- to below-ground biomass (shoot/root ratio, [S/R]) was calculated as the total dry mass of leaves plus stems (or stolons) divided by the dry mass of the below-ground system (rhizomes, bulbs, and roots) (Table 2.2). The mass of reproductive tissues was not included in the ratio because of species' differing flowering phenology. Some species had passed their peak bloom time when sampling began and already had mature fruits, while others had just started to flower, thus reproductive mass was not comparable.

Clonality was treated as an ordinal trait; species were assigned one of three values; 0 = non-clonal, 0.5 = limited clonality (via short rhizomes or branching caudices), or 1 = strongly clonal (via rhizomes or stolons), based on field excavations and descriptions in regional floras (Hitchcock and Cronquist 1973, Pojar and MacKinnon 1994, Baldwin et al. 2012; Table 2.1).

Data analyses

Cover-light relationship as an index of sensitivity to encroachment. We used the subplot-scale measurements of species cover and light to develop a quantitative index of sensitivity to encroachment (SEI). For each species, data were combined from the 2004 and 2014 samples, with the following exceptions. Data for *Fragaria virginiana* were from 2014 because in 2004, *F. virginiana* was not distinguished from its congener, *F. vesca*. Data for the grass species, *Bromus carinatus*, *Danthonia intermedia*, and *Festuca idahoensis*, were from 2004 because only forbs were sampled in 2014. Finally, data for *Calochortus subalpinus* were from 2004 because plants were senescent at the time of sampling in 2014.

Our quantitative index describing species sensitivity was computed from the coefficient of variation (CV; standard deviation divided by the mean) of cover across the light gradient. Specifically, for each species, we fit a local polynomial regression model, regressing non-zero values of cover (%) on total transmitted light (range of light values: 14.5 to 88.3%) using the loess function in the stats package in R (R Core Team 2013). We used a large smoothing parameter (1) for the spline function to avoid over fitting the data. The local model allowed the distributions of species cover-light relationship to vary (e.g., initial increase then decline, a linear decline, or an exponential decline), rather than forcing the data to fit into a single model form. Finally, we computed species CVs from the predicted values of cover at 0.1% increments of light (14.5 to 88.3%, the range in which all species were present). Simulations confirmed that the CV accurately captures the magnitude of variation in cover (sensitivity to light), when cover-light relationships take different forms: exponential declines yielded higher CVs than did linear or quadratic declines (Appendix Fig. A3). Our interpretation thus follows that species with an exponential decline in cover have a larger CV value and thus a higher SEI and are considered more sensitive to encroachment whereas those with a smaller CV are less sensitive, and have a lower SEI.

Trait-light relationship as a measure of trait variation. In contrast to the CV as an index of sensitivity, we expressed the magnitude of trait variation by the linear slope (β_1) of the relationship between light and species' trait values (Ackerly and Cornwell 2007). This allowed us to account not only for the magnitude of change, but the direction of change over the light gradient, which for some traits differed among species (increasing or decreasing in the shade). Thus, we could distinguish between adaptive responses to shading (e.g., an increase in SLA or S/R, giving rise to a negative slope) and those indicative of shade intolerance (e.g., a decrease in shoot height or SLA, giving rise to a positive slope). All linear models were made using the lm function in the stats package in R (R Core Team 2013). For each of the principal traits (SLA, S/R, and shoot height) and their components (leaf area, leaf mass, above and below ground biomass), we regressed each species trait values as a function of light (*n* = 15-17 individuals per species).

Relationships between sensitivity (SEI) and trait variation. For each trait (except clonality), we tested the hypothesized negative relationship (*H1*) between SEI and trait variation using Pearson's correlations for our 13 focal species. To determine whether SEI differed among species with varying clonal potential, we conducted a Kruskal-Wallis test on the mean SEI of each group (*n* = 2 to 6 species per group; Table 2.1) using the kruskal.test function in the stats package in R (R Core Team 2013). I chose to use a Kruskal-Wallis test on the mean SEI of clonal groups rather than an ANOVA because clonal groups did not meet the assumptions of ANOVA and Kruskal-Wallis tests allow for the comparison of groups that do not meet the assumptions of normality and have unequal variance.

We then tested the hypothesized role of encroachment as a filter on the functional trait composition of meadow species (*H2*). We predict that reduced light would reduce the abundance of non-clonal species and those with limited variation in traits considered advantageous to light capture. First, using matrix multiplication, we generated a subplot x trait-variation matrix that integrated the relative abundance of species with differing trait values (McCune and Grace 2002). Specifically, we multiplied the 617 subplot x 13 species cover matrix (species' cover from 2004/2014) by a 13 species x 8 trait-variability/clonality matrix using the base package in R (R Core Team 2013). Resulting values were divided by the summed cover of meadow species within a subplot, yielding abundance-weighted averages (McCune, in review) for 617 subplots by 8 traits (trait variabilities and clonality). For traits with continuous values, subplot scores could range from negative to positive, reflecting the relative abundance of species with contrasting responses to shading (i.e., an increase or decrease in intraspecific trait variation). For clonality, subplot scores ranged from 0 to 1, reflecting the relative abundance of species with varying clonal potential (0 = all non-clonal species, 1 = all highly clonal species). Finally, each column of the subplot x trait-variation matrix was regressed against the corresponding value of transmitted light (%) for each plot to assess the functional composition of species across the encroachment gradient.

RESULTS

Species sensitivity to encroachment (light)

Light transmittance ranged from 7.1 to 94.3% among subplots (mean= 38%, sd= 24). Species' cover also varied substantially (range= 0.1 to > 40%, mean= 3.7, sd=5.3) as did species' responses to light (Fig. 2.1; Appendix Table A1). Sensitivity to encroachment index varied more than three-fold among species (range= 22 to 79, mean= 40, sd= 18; Fig. 2.1). Among the least sensitive species—*Iris chrysophylla*, *Achillea millefolium,* and *Bromus carinatus*—cover changed little over the light gradient. In contrast, among the most sensitive species—*Lupinus latifolius, Calochortus subalpinus*, and *Orthocarpus imbricatus*—cover declined steeply to consistently low levels in the shadiest environments (Fig. 2.1; Appendix Table 1A).

Relationships between sensitivity to light and variability in trait expression (H1)

We found no support for the hypothesis that SEI is greater in species with less variation in trait expression across the light gradient.

Specific leaf area. Sensitivity was not correlated with variation in SLA (r= -0.44, p-value= 0.14, Fig. 2.2). When we excluded the annual, *Orthocarpus imbricatus* (an outlier for SLA), the correlation remained non-significant and reversed in slope (r= 0.24, p-value= 0.46, Fig. 2.2b). Although individual species showed the expected response to light—increasing SLA in the shade (Table 2.3, Appendix Fig. A4)—the magnitude of change, as measured by the slope did not correlate with SEI. To better understand the lack of correspondence between SEI and variation in SLA, we separately examined the components of SLA: leaf area and leaf mass. We then tested whether intraspecific variation in these traits was correlated with SEI. Sensitivity was positively correlated with intraspecific variation in leaf area (Fig. 2.2c). Leaf area increased in the shade for species with low SEI (e.g., *Achillea millefolium* and *Bromus cariantus*), but changed little or declined in the shade for those with high SEI (e.g., *Orthocarpus imbricatus* and *Calochortus subalpinus*) (Table 2.3, Appendix Fig. A5). In contrast, SEI did not correlate with variation in leaf mass. For most species, leaf mass changed at low rates with increasing shade (Table 2.3, Appendix Fig. A6).

Shoot/root ratio. For all but 2 species, S/R did not vary with light (Table 2.4, Appendix Fig. A7), thus the relationship with SEI was not tested (see Appendix Fig. A8). The alteration in biomass allocation varied in opposite directions for the 2 species where S/R changed over the light gradient: allocation to shoots increased in the shade for *Iris chrysophylla*, but decreased in the shade for *Achillea millefolium* (Table 2.4). Limited intraspecific variation in biomass allocation among most species reflects a common trend of decline (or occasionally no change) in both shoot and root mass over environmental gradients (Table 2.4, Appendices Fig. A9 and A10); in sum, most species simply declined in total mass with little change in biomass allocation (Table 2.4, Appendix Fig. A11).

Shoot height. Species showed substantial variation in shoot height with changes in light. However, this variability did not correlate with SEI (Fig. 2.3). Some species responded as expected, etiolating in the shade, but others became shorter (Table 2.4, Appendix Fig. A12).

Clonality. There was no difference in the mean SEI of different clonal groups (non-clonal, limited clonality, and strongly clonal) (Fig. 2.4; Kruskal-Wallis test, $X^2 = 2.1$, $df = 2$, $p = 0.34$).

Encroachment as a filter on the functional composition of the meadow species (H2)

We hypothesized that encroachment would act as a filter on the functional composition of meadow species, reducing in the shade the abundance of species with limited trait variation. Results did not show support for this prediction. As light levels declined, subplot communities were characterized by increasing variation in the relative abundance of species with more and less intraspecific variation for a trait (Fig. 2.5; Pearson's correlation coefficients between trait variability and light: SLA=0.16, leaf area=0.14, leaf mass=0.36, S/R=0.21, Shoot mass= 0.22, root mass= 0.17, shoot height=0.02) and of clonal and non-clonal species (Fig. 2.5; Pearson's correlation coefficients between clonality and light= 0.18). The nature of this variation (adaptive or not) and its range varied among traits, depending on the consistency and magnitude among species trait-light relationship (e.g., consistent and adaptive response for SLA vs. a mix of adaptive and stress responses for leaf area and shoot height). The effect was weaker for SLA and S/R, traits that showed less variability among species across the light gradient.

DISCUSSION

Conifer encroachment over the past century has reduced both the extent and habitat quality of meadows in the Oregon Cascade Range (Dailey 2007, Takaoka and Swanson 2008, Haugo et al. 2011). Although gradual conversion to forest reduces the overall abundance and diversity of meadow species, species show surprising variation in their rates of decline (Haugo and Halpern 2007). We sought to understand whether the degree of intraspecific variability in morphological traits related to light capture, the resource thought to be most limiting beneath the canopy of trees, could explain the interspecific variation in species response to encroachment. We hypothesized (*H1*) that species' SEI varies inversely with intraspecific trait variation for those traits that involve light capture and carbon gain. Our comparison of variation in functional traits of 13 species with widely varying SEI reveals little to no correlation between species trait variability and among species variation in SEI for the traits considered: SLA, S/R, shoot height, and clonality. Although some species displayed pronounced intraspecific variation in some traits, others did not, and the direction or relative magnitude of trait variation among species was not consistent with SEI.

All species showed an increase in SLA with a reduction in light, a common response of most species to shading (Wright and Westoby 1999, Ackerly et al. 2002, Burns 2004). For a given investment in leaf mass, an increase in leaf area increases the area available for light capture, which is critical as light becomes limited. Although species showed substantial variation in their responses, greater observed intraspecific variability in SLA did not correlate with greater tolerance of shade (i.e. species with lower SEI values). Variation in leaf area alone was a stronger predictor of SEI. Species that developed larger leaves in the shade were less sensitive to shading; species that developed smaller leaves, were more sensitive. Less sensitive species thus appear to show changes in leaf form that are adaptive in the shade—increasing in size, while decreasing in mass (Gianoli et al. 2012, Gianoli and Saldana 2013). In contrast, although SLA increased in the shade for more sensitive species, it was due to a larger decline in leaf mass than in area. Although this may reduce metabolic costs, it does not necessarily enhance carbon gain. Ultimately, our ability to interpret the relevance of leaf area variation among species may be limited by the fact that the metric used to rank sensitivity, SEI, is predicated on plant cover, which is likely correlated to leaf area.

We predicted that sensitivity would be greater in species less able to adjust allocation of biomass from root systems to shoots and leaves. However, most species showed little change in allocation patterns across the light gradient, instead losing mass proportionately from above- and below-ground structures. This could suggest that our target species lack the ability to alter their allocation of biomass across an environmental gradient. Alternatively, that species did not shift allocation to above-ground structures could suggests that resources other than light are limiting in encroached forest. In studies of forest-meadow edges in this system, Griffith et al. (2005) found that although soil moisture increased, nitrogen availability decreased significantly from open meadow to forest. Alternatively, if meadow species have evolved in environments in which competition for soil resources is stronger than competition for light, constraints in root-system morphology may limit plasticity in allocation. For the two low SEI species that showed significant variation in S/R, their responses differed: allocation to shoots increased in the shade in *Iris chrysophylla* but decreased in the shade in *Achillea millefolium*. For *Achillea*, declines for shoot and root mass were non-significant, but relative declines differed, leading to a significant reduction in the ratio. In contrast, in *Iris*, declines in shoot and root mass were both significant, but loss of root mass was much greater (almost seven times that of leaves). These patterns suggest contrasting strategies for persistence given the morphological constraints of these species. In open-meadow conditions, *Iris* develops a dense and massive rhizome system giving rise to the smallest S/R of the study species (Table 2.3). These provide a substantial reserve of carbohydrates, which are gradually depleted in the shade (Zobel and Antos 1987). In contrast, *Achillea* has a system of long slender rhizomes that are advantageous to foraging and ramet production, but contribute less to storage. The greater decline in shoot mass reflects the fact that shoot production is dependent, in large part, on reproduction, and flowering shoots are rarely initiated in the shade (Zeevart 1969, Celis et al. unpublished manuscript). The greater allocation to root systems may thus be a developmental or morphological constraint.

Sensitivity to encroachment was unrelated to variation in shoot height across the light gradient, counter to expectation. Some species produced longer (etiolated) shoots in the shade as expected (Kroon and Hutchings 1995). Others produced shorter shoots, suggesting limited ability to respond to changes in the ratio of red to far red light under the canopy (e.g., Mulligan et al. 1997). Alternatively, differences in variation in shoot height among species may relate to differences in the ability to produce flowering shoots in the shade (Lettow et al. 2014, Celis et al. unpublished manuscript). Similarly, we were unable to demonstrate a significant relationship between clonality and SEI. It is possible that a larger, more balanced sample of species would have produced stronger differences among groups. Alternatively, species with limited clonal potential may survive shading through other mechanisms, including changes in leaf morphology (leaf shape or area) or changes in biochemistry (chlorophyll a/b ratio; Pearcy and Sims 1994) or a greater ability to utilize light in the forest understory (Gianoli and Saldana 2013).

We also hypothesized (*H2*) that encroachment would act as an “environmental filter” on the functional composition of residual meadow species—reducing the abundance of non-clonal species and those with limited variation in trait expression. Counter to expectation, reduced levels of light did not homogenize the functional composition of shaded subplots. Rather, for most traits, it increased the heterogeneity of trait variability, giving rise to subplots dominated either by “high-” or “low-variability” species, or both. This heterogeneity could suggest greater variability of resource conditions in the shade (both above and below ground). However, it is also likely to reflect the abundance-weighted averaging of trait scores within subplots—averages based on increasingly fewer (often one or two) meadow species in shaded subplots and thus to the trait values of those species (including extremes). Subplots showed considerably less heterogeneity for SLA and S/R, traits for which species showed more comparable variation in their relationship with light.

CONCLUSIONS

Differences in morphological variability (reflecting either phenotypic plasticity or ecotypic variation) offer limited insight into the sensitivity of meadow species to conifer encroachment. However, we did find that more sensitive species tend to develop smaller leaves in the shade whereas less sensitive species develop larger leaves; a response that could allow less sensitive species to more effectively capture light resources as they are limited by conifer encroachment. Our results point to the limited ability of soft traits to predict species and community responses to encroachment in the meadows examined. Ultimately, soft traits are used as proxies for more difficult to measure physiological and demographic responses. Therefore, it is possible that intraspecific variation in physiological adaptions to the light environment, or hard traits, that were not considered in this study may be more important to species' survival, and clearly warrant further study. For example, Saldana et al. (2005) were able to detect the shade tolerance levels of three *Blechnum* species by measuring their photosynthetic capacity and dark respiration rate, using a portable infrared gas analyzer and leaf chamber, over a light gradient. At the same time, we have assumed, both in our index of sensitivity and assessment of trait variation, that species' distributions (or niche breadth) are driven primarily by responses to light. Although conifer encroachment of meadows substantially reduces the availability of light, it also effects major changes in litter quality, soil biochemistry (Griffiths et al. 2005), and the abundance and composition of microbial and fungal communities (Kageyama et al. 2008). Understanding how changes in these factors, in addition to light, affect meadow species survival, may be critical to interpreting their differing responses to encroachment.

ACKNOWLEDGEMENTS

Thank you to the Andrews Forest LTER grant (Award No. DEB-0823380), The Portland Garden Club Katherine Pamplin Scholarship, and Moldenke Scholarship for financial support for this project. Bruce McCune and Ariel Muldoon provided critical statistical advising. We whole-heartedly thank Katherine Dymek and Chris Parson for field and laboratory assistance. FAJ acknowledges support from the National Science Foundation (DEB1257976 and DEB1457837) and Oregon State University.

LITERATURE CITED

Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K., and Starmer, K.P. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia,* **130**, 449-457.

Ackerly, D.D., and Cornwell, W. (2007). A trait based approach to community assembly: partitioning of species trait values into within- among-community components. *Ecology Letters*, **10**, 135-145.

Antos, J.A., and Zobel, D.B. (1984). Ecological implications of below ground morphology of nine coniferous forest herbs. Botanical Gazette, **145**, 508–517.

Archer, S., Schimel, D.S., and Holland, E.A. (1995). Mechanisms of shrubland expansion: land use, climate or CO_2? *Climate Change,* **29**, 91-99.

Baldwin, B. B., Goldman, D., Keil, D., Patterson, R., Rosatti, T., and Wilken, D. (2012). The Jepson manual: vascular plants of California, second edition. University of California Press: Berkeley, Ca.

Bloom, A.J., Chapin, F.S. III, Mooney, H.A. (1985). Resource limitation in plants: an economic analogy. *Annual Review of Ecology and Systematics,* **6**, 363–392.

Briggs, J.M., Knapp, A., Blair, J., Heisler, J., Hoch, G., Lett, M., and McCarron, J. (2005). An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic Grassland to Shrubland. *BioScience*, **55**, 243-254.

Bunchgrass Ridge: Study Area (2005). Retrieved from http://depts.washington.edu/bgridge/B.Study-area/B.Study-area.htm#Soils

Burns, K.C., 2004. Patterns in specific leaf area and the structure of a temperate heath community. *Diversity and Distributions* **10**:105-112.

Castro-Diez, P. (2012). Functional trait analyses: Scaling up from species to community level. *Plant Soil* **357**: 9-12.

Celis, J., Halpern, C.B., and Jones, F.A. (unpublished manuscript). Consequences of reduced light for flower production in conifer-invaded meadows of the Pacific Northwest, U.S.A.

Cingolani A.M. Cabido, M., Gurvich, D.E., Renison, D., and Diaz, S., 2007. Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? *Journal of Vegetation Science* **18**: 911-920.

Cornwell, W. and Ackerly, D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* **79**: 109-126.

Dailey, M.M. (2007). Meadow Classification in the Willamette National Forest and Conifer Encroachment Patterns in the Chucksney-Grasshopper Meadow Complex, Western Cascade Range, Oregon. (Master's Thesis). Retrieved from Oregon State Student Archives.

Dong, M. (1992). Morphological plasticity of the clonal herb *Lamiastrum galeobdolon* (L.) Ehrend. & Polatschek in response to partial shading. *New Phytologist* **124**: 291-300.

Frazer, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Gianoli, E., Saldana, A., and Jimenez-Castillo, M. (2012). Ecophysiological traits may explain the abundance of climbing plant species across the light gradient in a temperate rainforest. *Plos ONE* **7**, e38831.

Gianoli, E., and Saldana, A. (2013). Phenotypic selection on leaf functional traits of two congeneric species in a temperate rainforest is consistent with their shade tolerance. *Oecologia* **173**: 13-21.

Gleeson, S.K. and Tilman, D. (1992). Plant allocation and the multiple limitation hypothesis. *The American Naturalist* **139**: 1322-1343.

Griffiths, R., Madritch, M., and Swanson, A. (2005). Conifer invasion of meadows transforms soil characteristics in the Pacific Northwest. *Forest Ecology and Management* **208**: 347-358.

H. Wickham. ggplot2: elegant graphics for data analysis. Springer New York, 2009.

Halpern, C. B., Haugo, R., Antos, J., Kaas, S., and Kilanowski, A. (2012). Grassland restoration with and without fire: evidence from a tree-removal experiment. *Ecological Applications* **22**: 425-441.

Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K., Ni, J., and Sutra, J.P. (2010). Ecophysiological and bioclimatic foundations for global plant functional classification. *Journal of Vegetation Science* **21**: 300-317.

Haugo, R. D., and Halpern, C. B. (2007). Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Botany* **88**: 285-298.

Haugo, R. D., and Halpern, C. B. (2010). Tree age and tree species shape positive and negative interactions in a montane meadow. *Botany* **88**: 488-499.

Haugo, R. D., Halpern, C. B., and Bakker, J. D. (2011). Landscape context and long-term tree influences shape the dynamics of forest-meadow ecotones in mountain ecosystems. *Ecosphere* **2**(8): art 91.

Highland, S. and Jones, J. (2014). Extinction debt in naturally contracting mountain meadows in the Pacific Northwest, USA: varying response of plants and feeding guilds of nocturnal moths. *Biodiversity Conservation* **23**: 2529-2544.

Hirose, T. and Werger, M.J.A. (1995). Canopy structure and photon flux partitioning among species in a herbaceous plant community. *Ecology* **76**: 466-474.

Hitchcock, C.L., and Cronquist, A. (1973). Flora of the Pacific Northwest. University of Washington Press, Seattle, Wash.

Hulshof, C.M. and Swenson, N.G. (2010). Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology* **24**: 217-223.

Humphrey, D., and Pyke, D. (1997). Clonal foraging in perennial wheatgrasses: a strategy for exploiting patchy soil nutrients. *Journal of Ecology* **85**: 601-610.

Ikuaniece, S., Brumelis, G., Kasparinskis, R., Nikodemus, O., Straupe, I., and Straupe, J. (2013).

Effects of soil and canopy factors on vegetation of *Quercus robur* woodland in the boreo-nemoral zone: a plant-trait based approach. *Forest Ecology and Management* **295**: 43-50.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. (2010). Intraspecific variability and trait-based commnity assembly. *Journal of Ecology* **98**: 1134-1140.

Kageyama, S.A., Posavats, N.R., Waterstripe, K.E., Jones, S.J., Bottomley, P.J., Cromack Jr., K., and Myrold, D.D. (2008). Fungal and bacterial communities across meadow-forest ecotones in the western Cascades of Oregon. *Canadian Journal of Forest Research* **38**: 1053-1060.

Kroon, H.D. and Hutchings, M.J. (1995). Morphological plasticity in clonal plants: the foraging concept reconsidered. *Journal of Ecology* **83**: 143-152.

Lettow, M.C., Brudvig, L.A., Bahlai, C.A., and Landis, D.A. (2014). Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management* **329**: 89-98.

Lezberg, A.L., Antos, J., and Halpern, C. (1999). Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula. *Canadian Journal of Botany* **77**: 936-943.

Loupre, P., Bittebiere, A.K., Clement, B., Pierre, J.S., and Mony, C. (2012). How past and present influence the foraging of clonal plants? *PlosOne* **7**: e38288.

McAlpine, K.G. and Jesson, L.K. (2007). Biomass allocation, shade tolerance and seedling survival of the invasive species *Berberis darwinii* (Darwin's barberry). *New Zealand Journal of Ecology* **31**: 1-12.

McCain, C., Halpern, C.B. & Lovtang, S. (2014) Non-forested plant communities of the northern Oregon Cascades. USDA Forest Service, Pacific Northwest Region, Technical Paper R6-ECOL-TP-01-14.

McConnaughay, K.D.M., and Coleman, J.S. (1999). Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* **80**: 2581-2593.

McCune, B., in review ms. Variations in the sample unit by trait matrix in community ecology.

McCune, B., and Grace, J. (2002). Analysis of Ecological Communities. MjM Software Design. Glenden Beach, OR 97388.

Messier, J., McGill, B.J., and Lechowicz, M.J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838-848.

Miller, E.A., and Halpern, C.B., 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetative Science* **9**: 265–282.

Mulligan, M., Chory, J., and Ecker, J. (1997). Signaling in plants. *PNAS* **94**: 2793-2795.

Osnas, L.D., Lichstein, J.W., Reich, P.B. and Pacala, S.W. (2013). Global leaf trait relationships: mass, area, and the leaf economic spectrum. *Science* **130**: 741-744.

Pearcy, R.W., and Sims, D.A. (1994). Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. Pages 145-174 *in* M.M. Caldwell and R.W. Pearcy (editors). Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground. Academic Press, San Diego, CA.

Petchey, O.L. and Gaston, K. (2006). Functional diversity: back to basics and looking forward. *Ecological letters* **9**: 741-758.

Pojar, J., and MacKinnon, A. (1994). Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia and Alaska. Lone Pine Publishing: Vancouver, British Columbia.

Poorter, L., (2001). Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Functional Ecology* **15**: 113-123.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rasband, W.S. (2014) ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.

Reich, P., Walters, M., and Ellsworth, D. (1997). From tropics to tundra: Global convergence in plant functioning. *Ecology* **94**: 13730-13734.

Rice, J., Halpern, C., Antos, J., and Jones, J., (2012). Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow. *Plant Ecology* **213**: 555-568.

Saldana A., Gianola, E., and Lusk, C.H. (2005). Ecophysiological responses to light availability in three *Blechum* species (Pteridophyta, Blechnaceae) of different ecological breadth. *Oecologica* **145**: 252-257.

Scholes, R.J. and Archer, S.R. (1987). Tree-grass interactions in savannas. *Annual Review of Ecological Systems* **28**: 517-544.

Silvertown J., Franco, M., Pisanty, I., and Mendoza, A. (2014). Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *British Ecological Society* **81**: 465-476.

Stueffer J.F., de Kroon, H., and During, H.J. (1996). Exploitation of environmental heterogeneity by spatial division of labour in clonal plant growth. *Functional Ecology* **10**: 328-334.

Suding, K., Lavorel, S., Chapin III, F.S., Cornelissens, J., Diaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S., and Navas, M.L. (2008). Scaling environmental change through the community level: a trait based response-and-effect framework for plants. *Global Change Biology* **14**: 1125-1140.

Svensson, B., Floderus, B., and Callaghan, T. (1994). *Lycopodium annotinum* and light quality: growth responses under canopies of two *Vaccinium* species. *Folia Geobotanica and Phytotaxinomica* **29**: 159-166.

Takaoka, S., and Swanson, F.J. (2008). Change in extent of meadows and shrub fields in the central western Cascade Range, Oregon. Prof. Geogr. **60**: 527-540.

USDA, NRCS. 2015. The PLANTS Database (http://plants.usda.gov, 24 April 2015). National Plant Data Team, Greensboro, NC 27401-4901 USA.

van Groenendael, J. & de Kroon, H. (eds) 1990: Clonal growth in plants: regulation and function. SPB Academic Publishing, The Hague.

Vale, T.R. (1981). Tree invasion of montane meadows in Oregon. *American Midland Naturalist* **105**: 61–125.

Violle, C., Enquist, B., McGill, B., Jiang, L., Albert, C., Hulsholf, C., Jung, V., and Messier, J. (2012). The return of variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27**: 244-252.

Western Regional Climate Center. 2011. Retrieved from http://www.wrcc.dri.edu/climatedata/comparative/

Wright, I.J. and Westoby, M. (1999). Differences in seedling growth behavior among species: trait correlations across species, and traits shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **81**: 85-97.

Zald, H.S.J. (2009). Extent and spatial patterns of grass bald land cover change (1948-2000), Oregon Coast Range, USA. *Plant Ecology* **201**:517-529.

Zeevart, Jan A. D. (1962). Physiology of flowering: flowering is hormonally controlled, but the nature of hormones remains to be elucidated. *Science* **137**: 723-731.

Zobel, D.B. and Antos, J.A. (1987). Composition of rhizomes of forest herbaceous plants in relation to morphology, ecology, and burial by tephra. *Botanical Gazette* **148**: 490-500.

FIGURES

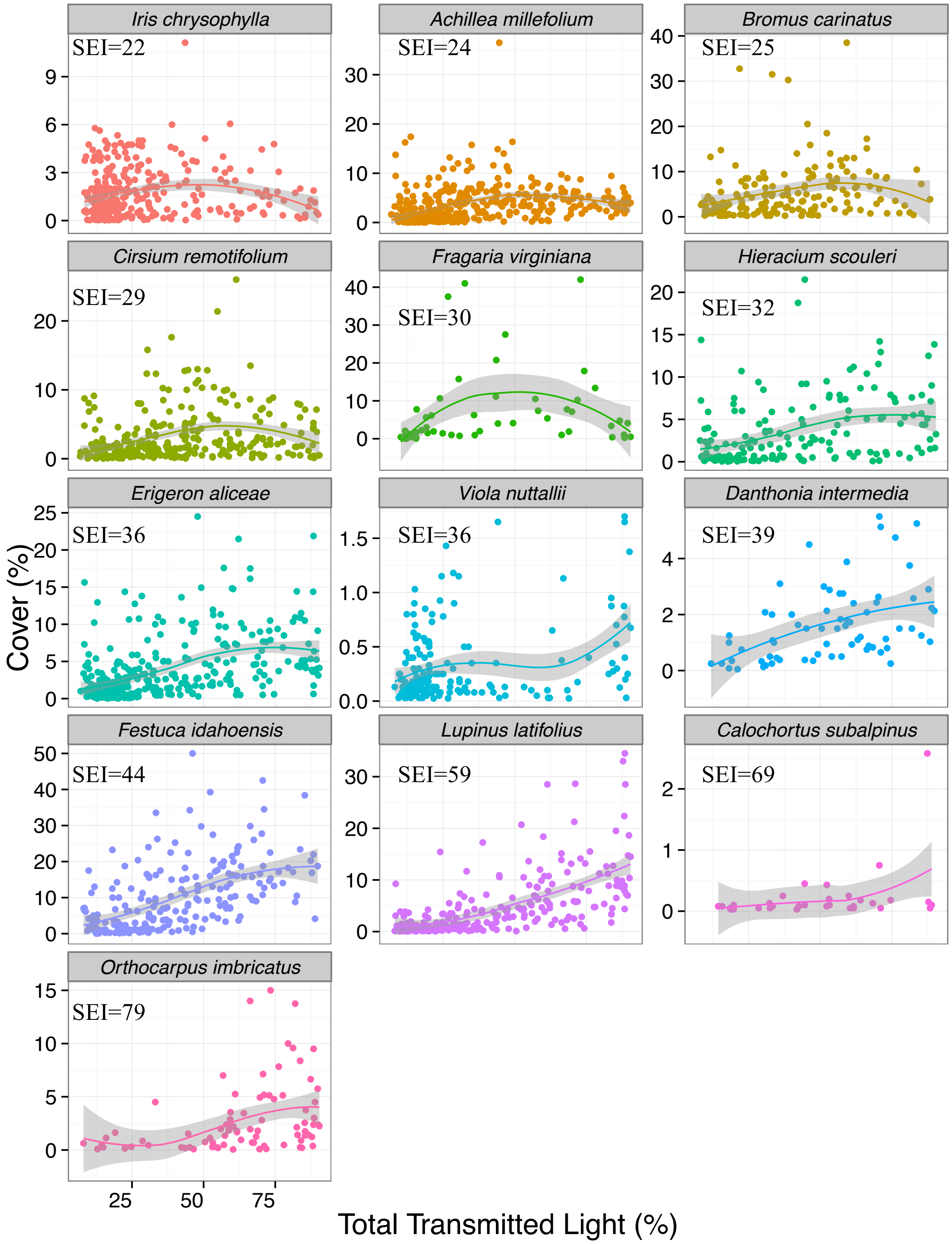

Figure 2.1. Cover-light relationships based on local polynomial regression models. Sensitivity to encroachment index (SEI) is the coefficient of variation (standard deviation divided by the mean, [CV]) of predicted cover (colored lines in graphs) across the range of light values where all species were sampled. Species are ordered left to right by SEI (low sensitivity to high). Gray bands represent confidence intervals. Cover scales vary to emphasize changes in cover across the light gradient rather differences among species.

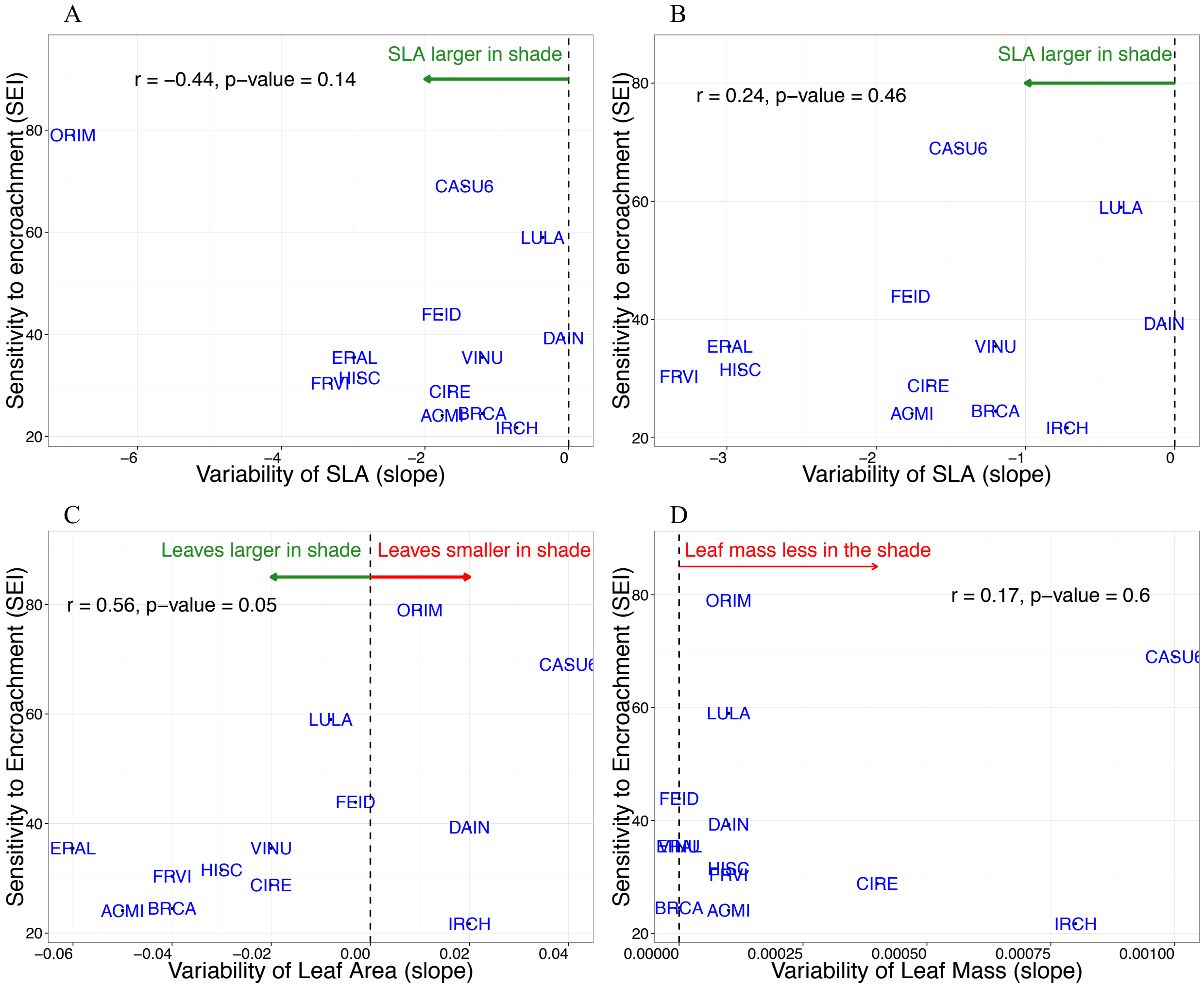

Figure 2.2. Relationships between variability in leaf traits (predicted slope of simple linear regressions for leaf trait-light relationship) and sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship). Full names of species are in Table 1. Dashed vertical lines indicates no variation in a trait across the light gradient (zero slope); negative values represent adaptive responses to shading. Relationships are shown for (A) Specific leaf area (SLA; leaf area: mass ratio) all species included; (B) SLA, *Orthocarpus imbricatus* (ORIM) excluded; (C) leaf area, all species included; and (D) leaf mass, all species included.

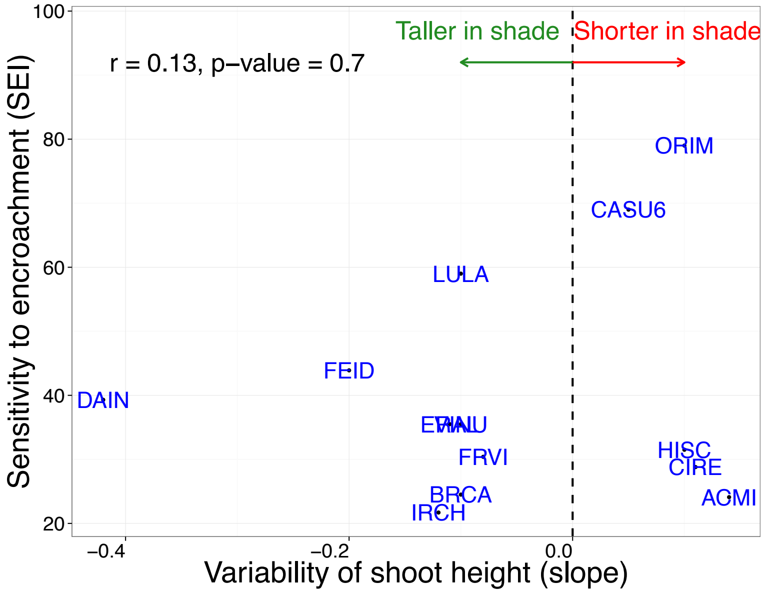

Figure 2.3. Relationships between variability in shoot height (simple linear regression slope of the shoot height-light relationship) and sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship). Full names of species are in Table 1. Dashed vertical line indicates no variation in shoot height across the light gradient (zero slope).

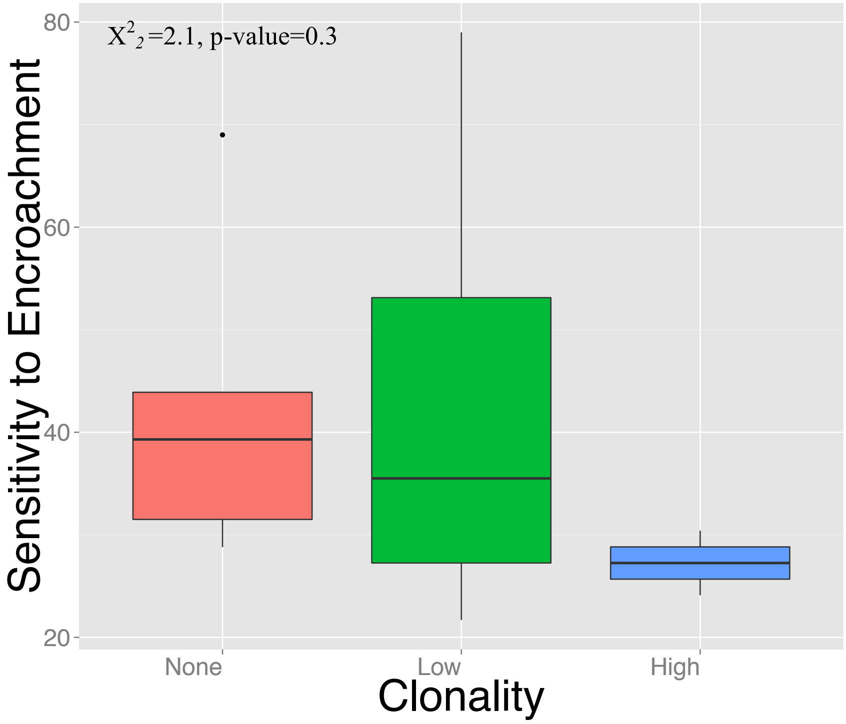

Figure 2.4. Mean sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship) of clonal groups. Groups are: none = non-clonal (*n* = 5), low = limited clonality (via short rhizomes or branching caudices; *n* = 7), and high = strongly clonal (via rhizomes or stolons; *n* = 2). Sensitivity does not differ among groups. Boxes span the range of the upper and lower quantile. Dark lines within the boxes represent the mean SEI of each clonal group and whiskers represent standard deviation.

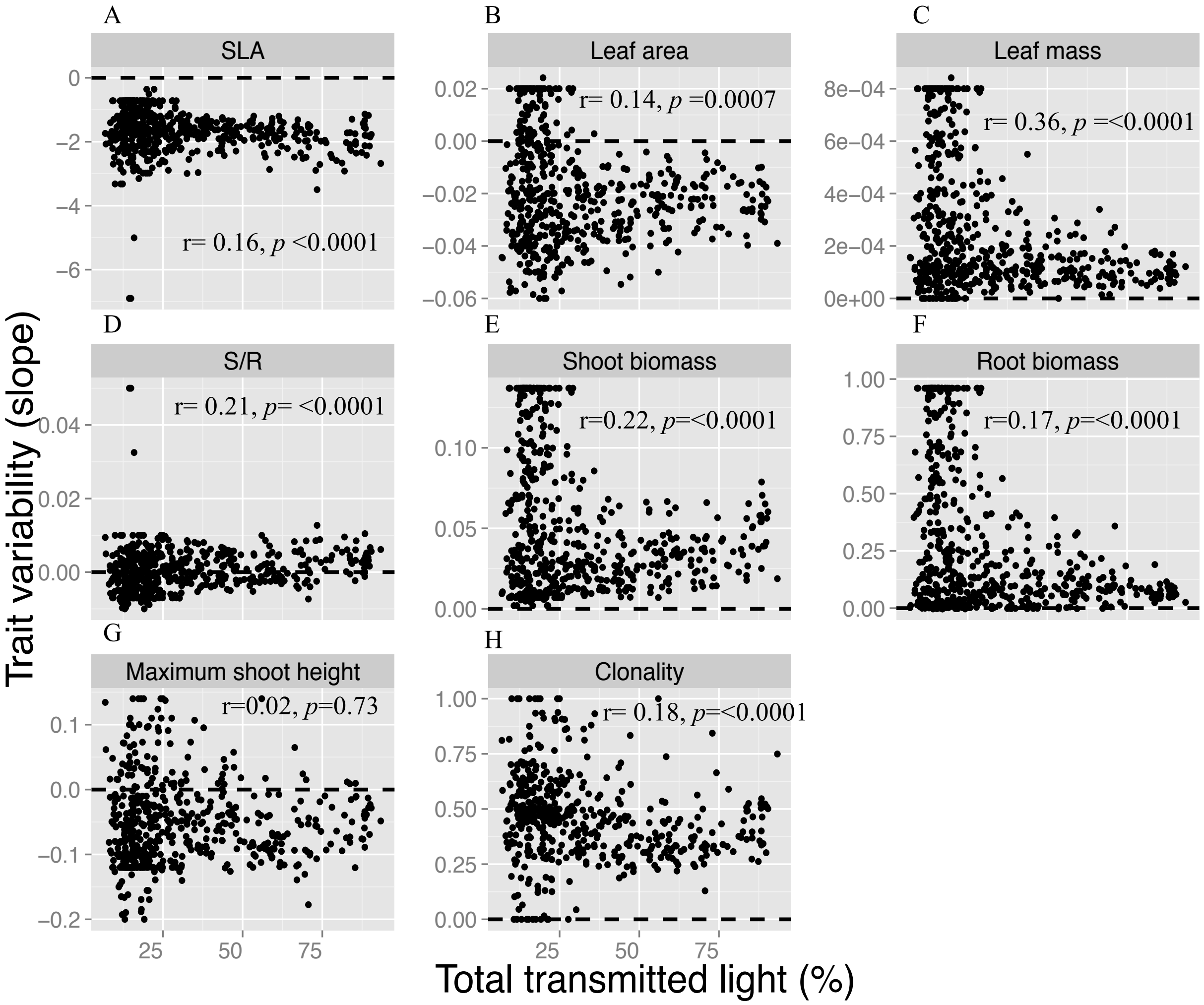

Figure 2.5. Relationship between subplot trait variability scores and light (r = Pearson correlation coefficient for n = 617). Each point represents a subplot score of trait variability given the relative abundance of species present and their level of trait variability. Relationships are shown for (A) Specific leaf area (SLA; leaf area: mass ratio), (B) leaf area, (C) leaf mass, (D) Shoot/Root ratio (S/R; biomass of leaves and stems: mass of root systems ratio), (E) Shoot biomass (dry mass of leaves and stems), (F) Root biomass (dry mass of root systems), (G) Maximum shoot height, and (H) Clonality (0 [non-clonal]-1[somewhat and strongly clonal]). Horizontal dashed lines indicate complete dominance of species with no variability in a trait. Trait variability above the line indicates a positive trait-light relationship, below the line indicates a negative trait-light relationship.

TABLES

Table 2.1. Basic growth-form and life-history traits of the study species sampled at Bunchgrass Ridge located on the western slope of the high Cascade Range, Oregon. Sample sizes are the numbers of individuals measured for functional traits. Clonality is rated as: 0 = non-clonal, 0.5 = limited clonality (via short rhizomes or branching caudices), or 1 = strongly clonal (via rhizomes or stolons).

Species	**Code**	**Sample size**	**Growth form**	**Longevity**	**Clonality**
Achillea millefolium	ACMI	16	forb	perennial	1
Bromus carinatus	BRCA	16	grass	perennial	0.5
Calochortus subalpinus	CASU6	16	forb	perennial	0
Cirsium remotifolium	CIRE	16	forb	perennial	0
Danthonia intermedia	DAIN	15	grass	perennial	0.5
Erigeron aliceae	ERAL	16	forb	perennial	0.5
Festuca idahoensis	FEID	17	grass	perennial	0
Fragaria virginiana	FRVI	16	forb	perennial	1
Hieracium scouleri	HISC	17	forb	perennial	0
Iris chrysophylla	IRCH	16	forb	perennial	0.5
Lupinus latifolius	LULA	15	forb	perennial	0.5
Viola nuttallii	VINU	15	forb	perennial	0.5
Orthocarpus imbricatus	ORIM	16	forb	annual	0

Table 2.2. Mean values and standard deviation (SD) of species' traits. Values for leaf traits are based on the averaged value of 1-5 healthy mature leaves per individual sampled. Specific leaf area (SLA) is the fresh leaf area divided by dry leaf biomass. Shoot to root ratio (S/R) is the dry mass of the leaves and stems divided by the dry mass of species' root systems.

			SLA (cm^2/g)		**Leaf area (cm^2)**		**Leaf mass (g)**		**S/R**		**Shoot mass (g)**		**Root mass (g)**		**Shoot height (cm)**	
Species	**Code**	**Sample size**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Achillea millefolium	ACMI	16	440.1	176.2	6.6	3.9	0.03	0.02	1.56	0.54	1.0	0.8	0.6	0.6	39.00	16.79
Bromus carinatus	BRCA	16	422.1	216.8	4.0	4.0	0.04	0.03	2.24	1.11	2.3	1.2	1.2	0.7	81.97	16.83
Calochortus subalpinus	CASU6	16	251.8	265.0	12.5	NA	0.09	NA	0.54	0.22	0.2	1.0	0.3	0.2	23.46	4.31
Cirsium remotifolium	CIRE	16	433.4	174.1	16.6	9.5	0.07	0.04	4.21	1.27	3.0	1.4	0.7	0.3	58.31	12.01
Danthonia intermedia	DAIN	15	259.5	172.0	1.9	0.7	0.02	0.006	1.22	0.72	1.2	0.6	1.6	1.4	49.07	13.38
Erigeron aliceae	ERAL	16	608.5	209.1	7.3	2.2	0.02	0.008	0.65	0.44	1.3	0.9	3.9	2.4	39.75	12.06
Festuca idahoensis	FEID	17	332.8	184.6	1.3	0.4	0.009	0.004	0.69	0.77	1.8	1.2	6.2	9.1	42.18	11.35
Fragaria virginiana	FRVI	16	506.6	249.3	5.5	1.6	0.02	0.007	1.48	1.28	0.7	0.4	0.7	0.7	15.11	4.27
Hieracium scouleri	HISC	17	648.0	175.5	7.7	3.0	0.03	0.01	0.28	0.09	0.8	0.7	0.13	2.9	26.76	6.10
Iris chrysophylla	IRCH	16	385.9	284.2	8.3	2.5	0.07	0.02	0.46	0.29	4.2	5.4	23.1	41.2	32.19	6.33
Lupinus latifolius	LULA	15	526.7	290.2	2.4	0.5	0.01	0.006	0.70	0.86	4.2	6.7	13.2	15.3	40.70	7.19
Viola nuttallii	VINU	15	536.5	187.4	5.3	1.7	0.02	0.007	1.67	2.60	0.2	0.2	0.2	0.1	12.73	4.90
Orthocarpus imbricatus	ORIM	16	719.3	165.6	1.1	0.2	0.003	0.007	7.60	3.75	0.2	0.2	0.03	0.02	26.88	3.76

Table 2.3. Coefficients, R^2, and significance of simple linear regression models of changes in leaf traits across the light gradient. Specific leaf area (SLA; leaf area: mass ratio). Species are ordered by sensitivity to encroachment (SEI, coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Significance is coded as: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

		SLA (cm^2/g)			**Leaf area (cm^2)**			**Leaf mass (g)**			
Species	**Code**	β_0	β_1	R^2	β_0	β_1	R^2	β_0	β_1	R^2	**df**
Iris chrysophylla	IRCH	167	-0.7	0.05	7.5	0.02	0.05	0.03	0.00084	**0.23***	14
Achillea millefolium	ACMI	317	-1.8	**0.53*****	9.1	-0.05	0.05	0.03	0.00012	0.05	14
Bromus carinatus	BRCA	300	-1.2	**0.30***	10.7	-0.04	0.01	0.05	-0.00006	0.06	12
Cirsium remotifolium	CIRE	307	-1.7	**0.66*****	17.6	-0.02	0.06	0.05	0.00041	0.10	14
Fragaria virginiana	FRVI	421	-3.3	**0.82*****	7.4	-0.04	**0.20***	0.02	0.00013	**0.30***	14
Hieracium scouleri	HISC	464	-2.9	**0.80*****	9.0	-0.03	**0.12***	0.02	0.00014	**0.30***	15
Erigeron aliaceae	ERAL	442	-3.0	**0.80*****	10.1	-0.06	**0.57*****	0.02	0.00001	0.07	14
Viola nuttallii	VINU	308	-1.2	**0.20***	6.2	-0.02	0.12	0.02	0.00001	0.08	13
Danthonia intermedia	DAIN	144	-0.07	0.09	0.9	0.02	**0.26***	0.007	0.00013	0.09	11
Festuca idahoensis	FEID	274	-1.8	**0.28***	1.5	-0.002	0.01	-0.005	0.00007	**0.23***	15
Lupinus latifolius	LULA	440	-0.4	**0.81*****	2.8	-0.01	**0.20***	0.003	0.00018	**0.30***	14
Calochortus subalpinus	CASU6	236	-1.5	**0.63*****	10.7	0.04	0.05	0.04	0.00089	**0.20***	13
Orthocarpus imbricatus	ORIM	909	-6.9	**0.32***	0.5	0.01	**0.20***	-0.003	0.00010	**0.48****	15

Table 2.4. Coefficients, R^2, and significance of simple linear regression models of changes in species' biomass traits across the light gradient. Shoot to root ratio (S/R; mass of leaves and stems: mass of root systems ratio). Shoot mass includes biomass of leaves and stems. Species are ordered by sensitivity to encroachment (SEI, coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Significance is coded as: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

		S/R			**Shoot mass (g)**			**Root mass (g)**			
Species	**Code**	β_0	β_1	R^2	β_0	β_1	R^2	β_0	β_1	R^2	**df**
Iris chrysophylla	IRCH	0.8	-0.0075	**0.46****	-2.19	0.14	**0.51****	-21.5	0.961	**0.42****	14
Achillea millefolium	ACMI	1.1	0.0107	**0.25***	0.70	0.007	0.04	0.55	0.002	0.01	14
Bromus carinatus	BRCA	1.9	0.0058	0.02	1.70	0.011	0.07	1.34	-0.003	0.02	14
Cirsium remotifolium	CIRE	3.8	0.0075	0.03	1.82	0.024	0.22	0.52	0.004	0.13	14
Fragaria virginiana	FRVI	1.0	0.0111	0.06	0.33	0.008	0.22	0.36	0.007	0.09	14
Hieracium scouleri	HISC	0.3	0.0005	0.02	-0.28	0.022	**0.74*****	-0.89	0.083	**0.65*****	15
Erigeron aliaceae	ERAL	0.9	-0.0048	0.12	1.00	0.007	0.07	1.48	0.035	0.21	14
Viola nuttallii	VINU	1.9	-0.0049	0.003	0.11	0.002	0.09	0.13	0.001	0.04	13
Danthonia intermedia	DAIN	1.8	-0.0101	0.11	1.12	0.001	0.002	1.04	0.010	0.03	13
Festuca idahoensis	FEID	1.3	-0.0110	0.11	0.44	0.025	**0.23***	-3.27	0.169	0.19	15
Lupinus latifolius	LULA	0.6	0.0022	0.01	-0.83	0.113	**0.26***	9.04	0.095	0.04	13
Calochortus subalpinus	CASU6	0.6	-0.0008	0.01	0.08	0.001	**0.20***	0.14	0.003	**0.15***	15
Orthocarpus imbricatus	ORIM	5.1	0.0530	0.05	-0.1	0.006	**0.50****	-0.01	0.001	**0.43****	14

Table 2.4. Continued

		Shoot height (cm)			**Total Biomass**			
Species	**Code**	β_0	β_1	R^2	β_0	β_1	R^2	**df**
Iris chrysophylla	IRCH	37.8	-0.12	**0.28***	-0.23	1.098	**0.45****	14
Achillea millefolium	ACMI	32.5	0.14	0.04	1.2	0.008	0.02	14
Bromus carinatus	BRCA	87.4	-0.10	0.03	3.0	0.008	0.02	14
Cirsium remotifolium	CIRE	53.2	0.11	0.06	2.4	0.028	0.21	14
Fragaria virginiana	FRVI	19.0	-0.09	**0.32***	0.7	0.015	0.17	14
Hieracium scouleri	HISC	22.3	0.09	0.18	-1.2	0.105	**0.66*****	15
Erigeron aliaceae	ERAL	44.7	-0.11	0.09	2.5	0.043	0.19	14
Viola nuttallii	VINU	16.6	-0.09	**0.35***	0.2	0.002	0.08	13
Danthonia intermedia	DAIN	72.2	-0.42	**0.57****	2.2	0.011	0.02	13
Festuca idahoensis	FEID	51.5	-0.17	0.12	-2.8	0.194	0.20	15
Lupinus latifolius	LULA	45.0	-0.10	0.26	8.2	0.208	0.09	13
Calochortus subalpinus	CASU6	20.8	0.05	0.10	0.2	0.005	0.22	15
Orthocarpus imbricatus	ORIM	20.2	0.11	**0.30***	-0.1	0.006	**0.52****	14

CHAPTER 3 General Conclusions

Encroachment of meadow communities by conifers has reduced the extent and quality of open habitat in the Cascade Range of Oregon (Dailey 2007, Takaoka and Swanson 2008, Haugo et al. 2011). While the overall abundance and richness of meadow species decline with tree establishment species show surprising variation in their rates of decline (sensitivity) (Haugo and Halpern 2007). Our research explored whether intraspecific variation in morphological traits related to the acquisition of light (the resource assumed to be most limiting in the understory) and clonal potential contribute to the relative sensitivity of species to encroachment. We predicted that species able to survive in the understory of the forest would display more intraspecific variation in specific leaf area (SLA, leaf area: leaf mass ratio), biomass allocation (S/R, shoot: root system ratio), shoot height, and clonality.

Although some traits of species varied significantly across the light gradient (e.g., SLA and shoot height), other traits changed little (e.g., shoot:root ratio). Moreover, the magnitude and direction of this variation generally did not correlate with species' sensitivity to encroachment. Although SLA increased in the shade for all species (an adaptive response), for more sensitive species this was due to a larger decline in leaf mass than in leaf area. Thus, when we examined leaf area variability we found that it was a better predictor of sensitivity. Those species that are more sensitive to tree establishment tended to have smaller leaves in the shade whereas species that are less sensitive tended to have larger leaves. This could suggest that less sensitive species are able to tolerate shade more given that they have a larger leaf with which to capture light. In the end, our ability to interpret the relevance of leaf area variation among species is limited by the fact that the metric used as proxy for sensitivity (SEI) is based on plant cover, which is correlated with leaf area. Future studies could control for this by using another measure of sensitivity, such as frequency, which would depend less on plant size than on presence/absence.

In addition, we found that instead of encroachment acting as a filter, reducing the representation of species with limited trait variability, it increased the heterogeneity of functional trait variation. The understory had both “high” and “low” intraspecific trait variation as well as clonal and non-clonal species. This heterogeneity of functional composition could indicate greater heterogeneity of resource availability in the forest understory (both above and below ground). However, it is also likely to reflect the abundance-weighted averaging of trait scores within subplots—averages are based on increasingly fewer meadow species in shaded subplots and thus are reflecting the trait values of sometimes only one or two species (including extremes).

Future studies examining differing rates of decline of meadow species following encroachment should focus their efforts on examining leaf traits. Specifically, intraspecific variation in physiological adaptions to the light environment that were not considered in this study including photosynthetic capacity and dark respiration rates (Saldana et al. 2005, Gianoli and Saldana 2013). In addition, our study focused on the effects of light availability on meadow species, and although light is greatly reduced following conifer encroachment, encroachment also alters litter quality, soil biochemistry, soil moisture availability (Griffiths et al. 2005), and the abundance and composition of microbial and fungal communities (Kageyama et al. 2008). Alternatively, our ability to examine the variation in species sensitivity through functional traits may be limited by the fact that intraspecific trait variation is less than interspecific trait variation (Cornwell and Ackerley 2007). The ability to successfully explain species responses to their environment using functional traits may be dependent on the scale at which one is examining community assembly.

My plan for future work in this system will include an examination of the rate of reproductive decline of meadow communities along a conifer encroachment gradient. We known that some meadow species can exist in encroached areas, but we do not know the extent to which tree encroachment is impeding residual meadow species' ability to reproduce. Our future research will quantify the changes in flower production across a conifer encroachment gradient at two sites in the western Cascade Range of Oregon: H.J. Andrews Experimental Forest and Bunchgrass Ridge. This work will allow us to infer the impacts of conifer encroachment on pollinator communities given their reliance on the flower production of meadow species.

BIBLIOGRAPHY

Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K., and Starmer, K.P. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia,* **130**, 449-457.

Ackerly, D.D., and Cornwell, W. (2007). A trait based approach to community assembly: partitioning of species trait values into within- among-community components. *Ecology Letters*, **10**, 135-145.

Antos, J.A., and Zobel, D.B. (1984). Ecological implications of below ground morphology of nine coniferous forest herbs. Botanical Gazette, **145**, 508–517.

Archer, S., Schimel, D.S., and Holland, E.A. (1995). Mechanisms of shrubland expansion: land use, climate or CO_2? *Climate Change,* **29**, 91-99.

Baldwin, B. B., Goldman, D., Keil, D., Patterson, R., Rosatti, T., and Wilken, D. (2012). The Jepson manual: vascular plants of California, second edition. University of California Press: Berkeley, Ca.

Baley, T. A., Totland, O., and Moe, S.R. (2013). Ecosystem responses to woody plant encroachment in a semiarid savanna rangeland. *Plant Ecology* **214**: 1211-1222.

Blom, C.W.P.M., Voesenek, L.A.C.J. (1996). Flooding: the survival strategies of plants. *Trees* **11**: 290-295.

Bloom, A.J., Chapin, F.S. III, Mooney, H.A. (1985). Resource limitation in plants: an economic analogy. *Annual Review of Ecology and Systematics,* **6**, 363–392.

Briggs, J.M., Knapp, A., Blair, J., Heisler, J., Hoch, G., Lett, M., and McCarron, J. (2005). An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic Grassland to Shrubland. *BioScience*, **55**, 243-254.

Brown, Joel R. and Carter, J. (1998). Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**:93-102.

Bunchgrass Ridge: Study Area (2005). Retrieved from http://depts.washington.edu/bgridge/B.Study-area/B.Study-area.htm#Soils

Burns, K.C., 2004. Patterns in specific leaf area and the structure of a temperate heath community. *Diversity and Distributions* **10**:105-112.

Castro-Diez, P. (2012). Functional trait analyses: Scaling up from species to community level. *Plant Soil* **357**: 9-12.

Celis, J., Halpern, C.B., and Jones, F.A. (unpublished manuscript). Consequences of reduced light for flower production in conifer-invaded meadows of the Pacific Northwest, U.S.A.

Cingolani A.M. Cabido, M., Gurvich, D.E., Renison, D., and Diaz, S., 2007. Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? *Journal of Vegetation Science* **18**: 911-920.

Cornwell, W. and Ackerly, D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* **79**: 109-126.

Dailey, M.M. (2007). Meadow Classification in the Willamette National Forest and Conifer Encroachment Patterns in the Chucksney-Grasshopper Meadow Complex, Western Cascade Range, Oregon. (Master's Thesis). Retrieved from Oregon State Student Archives.

Dong, M. (1992). Morphological plasticity of the clonal herb *Lamiastrum galeobdolon* (L.) Ehrend. & Polatschek in response to partial shading. *New Phytologist* **124**: 291-300.

Dussart, E., Lerner, P., and Peinetti, R. (1998). Long-term dynamics of two populations of Prosopis Caldenia Burkart. *Journal of Range Management* **51**: 685-691.

Frazer, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Gianoli, E., Saldana, A., and Jimenez-Castillo, M. (2012). Ecophysiological traits may explain the abundance of climbing plant species across the light gradient in a temperate rainforest. *Plos ONE* **7**, e38831.

Gianoli, E., and Saldana, A. (2013). Phenotypic selection on leaf functional traits of two congeneric species in a temperate rainforest is consistent with their shade tolerance. *Oecologia* **173**: 13-21.

Gleeson, S.K. and Tilman, D. (1992). Plant allocation and the multiple limitation hypothesis. *The American Naturalist* **139**: 1322-1343.

Griffiths, R., Madritch, M., and Swanson, A. (2005). Conifer invasion of meadows transforms soil characteristics in the Pacific Northwest. *Forest Ecology and Management* **208**: 347-358.

H. Wickham. ggplot2: elegant graphics for data analysis. Springer New York, 2009.

Halpern, C. B., Haugo, R., Antos, J., Kaas, S., and Kilanowski, A. (2012). Grassland restoration with and without fire: evidence from a tree-removal experiment. *Ecological Applications* **22**: 425-441.

Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K., Ni, J., and Sutra, J.P. (2010). Ecophysiological and bioclimatic foundations for global plant functional classification. *Journal of Vegetation Science* **21**: 300-317.

Haugo, R. D., and Halpern, C. B. (2007). Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Botany* **88**: 285-298.

Haugo, R. D., and Halpern, C. B. (2010). Tree age and tree species shape positive and negative interactions in a montane meadow. *Botany* **88**: 488-499.

Haugo, R. D., Halpern, C. B., and Bakker, J. D. (2011). Landscape context and long-term tree influences shape the dynamics of forest-meadow ecotones in mountain ecosystems. *Ecosphere* **2**(8): art 91.

Hickman, J.C. (1976). Non-forest vegetation of the western Cascade Mountains of Oregon. *Northwest Science* **50**: 145-155.

Highland, S. and Jones, J. (2014). Extinction debt in naturally contracting mountain meadows in the Pacific Northwest, USA: varying response of plants and feeding guilds of nocturnal moths. *Biodiversity Conservation* **23**: 2529-2544.

Hirose, T. and Werger, M.J.A. (1995). Canopy structure and photon flux partitioning among species in a herbaceous plant community. *Ecology* **76**: 466-474.

Hulshof, C.M. and Swenson, N.G. (2010). Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology* **24**: 217-223.

Humphrey, D., and Pyke, D. (1997). Clonal foraging in perennial wheatgrasses: a strategy for exploiting patchy soil nutrients. *Journal of Ecology* **85**: 601-610.

Ikuaniece, S., Brumelis, G., Kasparinskis, R., Nikodemus, O., Straupe, I., and Straupe, J. (2013). Effects of soil and canopy factors on vegetation of *Quercus robur* woodland in the boreo-nemoral zone: a plant-trait based approach. *Forest Ecology and Management* **295**: 43-50.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**: 1134-1140.

Kageyama, S.A., Posavats, N.R., Waterstripe, K.E., Jones, S.J., Bottomley, P.J., Cromack Jr., K., and Myrold, D.D. (2008). Fungal and bacterial communities across meadow-forest ecotones in the western Cascades of Oregon. *Canadian Journal of Forest Research* **38**: 1053-1060.

Kroon, H.D. and Hutchings, M.J. (1995). Morphological plasticity in clonal plants: the foraging concept reconsidered. *Journal of Ecology* **83**: 143-152.

Lettow, M.C., Brudvig, L.A., Bahlai, C.A., and Landis, D.A. (2014). Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management* **329**: 89-98.

Lezberg, A.L., Antos, J., and Halpern, C. (1999). Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula. *Canadian Journal of Botany* **77**: 936-943.

Loupre, P., Bittebiere, A.K., Clement, B., Pierre, J.S., and Mony, C. (2012). How past and present influence the foraging of clonal plants? *PlosOne* **7**: e38288.

McAlpine, K.G. and Jesson, L.K. (2007). Biomass allocation, shade tolerance and seedling survival of the invasive species *Berberis darwinii* (Darwin's barberry). *New Zealand Journal of Ecology* **31**: 1-12.

McCain, C., Halpern, C.B. & Lovtang, S. (2014) Non-forested plant communities of the northern Oregon Cascades. USDA Forest Service, Pacific Northwest Region, Technical Paper R6-ECOL-TP-01-14.

McConnaughay, K.D.M., and Coleman, J.S. (1999). Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* **80**: 2581-2593.

McCune, B., in review ms. Variations in the sample unit by trait matrix in community ecology.

McCune, B., and Grace, J. (2002). Analysis of Ecological Communities. MjM Software Design. Glenden Beach, OR 97388.

Messier, J., McGill, B.J., and Lechowicz, M.J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838-848.

Miller, E.A., and Halpern, C.B. (1998). Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetative Science* **9**: 265–282.

Moleele, N.M. and Perkins, J.S. (1998). Encroaching woody plant species and boreholes: is cattle density he main driving factor in the Oilfants Drift communal grazing land, south-eastern Botswana. *Journal of Arid Environments* **40**:245-253.

Mulligan, M., Chory, J., and Ecker, J. (1997). Signaling in plants. *PNAS* **94**: 2793-2795.

Osnas, L.D., Lichstein, J.W., Reich, P.B. and Pacala, S.W. (2013). Global leaf trait relationships: mass, area, and the leaf economic spectrum. *Science* **130**: 741-744.

Pearcy, R.W., and Sims, D.A. (1994). Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. Pages 145-174 *in* M.M. Caldwell and R.W. Pearcy (editors). Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground. Academic Press, San Diego, CA.

Petchey, O.L. and Gaston, K. (2006). Functional diversity: back to basics and looking forward. *Ecological letters* **9**: 741-758.

Pfeiffer, V. (2012). Influence of spatial and temporal factors on plants, pollinators, and plant-pollinator interactions in montane meadows of the western cascades. M.S. Thesis. Scholar's Archives. Oregon State University, Corvallis.

Pojar, J., and MacKinnon, A. (1994). Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia and Alaska. Lone Pine Publishing: Vancouver, British Columbia.

Poorter, L., (2001). Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Functional Ecology* **15**: 113-123.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rasband, W.S. (2014) ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.

Reich, P., Walters, M., and Ellsworth, D. (1997). From tropics to tundra: Global convergence in plant functioning. *Ecology* **94**: 13730-13734.

Rice, J., Halpern, C., Antos, J., and Jones, J., (2012). Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow. *Plant Ecology* **213**: 555-568.

Saldana A., Gianola, E., and Lusk, C.H. (2005). Ecophysiological responses to light availability in three *Blechum* species (Pteridophyta, Blechnaceae) of different ecological breadth. *Oecologica* **145**: 252-257.

Schleuning, M. and Matthies, D. (2008). Habitat change and plant demography: assessing the extinction risk of a formerly common grassland perennial. *Conservation Biology* **23**: 174-183.

Scholes, R.J. and Archer, S.R. (1987). Tree-grass interactions in savannas. *Annual Review of Ecological Systems* **28**: 517-544.

Silvertown J., Franco, M., Pisanty, I., and Mendoza, A. (2014). Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *British Ecological Society* **81**: 465-476.

Soudzilovskaia, N., Elumeeva, T., Onipchenko, V., Shidakov, I., Salpagarova, F., Khubiev, A., Tekeev, D., and Cornelissen, J. (2013). Functional traits predict relationship between abundance dynamic and long-term climate warming. *PNAS* **110**: 18180-1814.

Stueffer J.F., de Kroon, H., and During, H.J. (1996). Exploitation of environmental heterogeneity by spatial division of labour in clonal plant growth. *Functional Ecology* **10**: 328-334.

Suding, K., Lavorel, S., Chapin III, F.S., Cornelissens, J., Diaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S., and Navas, M.L. (2008). Scaling environmental change through the community level: a trait based response-and-effect framework for plants. *Global Change Biology* **14**: 1125-1140.

Svensson, B., Floderus, B., and Callaghan, T. (1994). *Lycopodium annotinum* and light quality: growth responses under canopies of two *Vaccinium* species. *Folia Geobotanica and Phytotaxinomica* **29**: 159-166.

Takaoka, S., and Swanson, F.J. (2008). Change in extent of meadows and shrub fields in the central western Cascade Range, Oregon. Prof. Geogr. **60**: 527-540.

Tilman D., May, R. M., Lehman, C. L., and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature* **371**: 65-66.

USDA, NRCS. 2015. The PLANTS Database (http://plants.usda.gov, 24 April 2015). National Plant Data Team, Greensboro, NC 27401-4901 USA.

Vale, T.R. (1981). Tree invasion of montane meadows in Oregon. *American Midland Naturalist* **105**: 61–125.

Violle, C., Enquist, B., McGill, B., Jiang, L., Albert, C., Hulsholf, C., Jung, V., and Messier, J. (2012). The return of variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27**: 244-252.

Waesch, G., and Becker T. (2009). Plant diversity differs between young and old mesic meadows in a central European low mountain region. *Agriculture, Ecosystems, and Environment* **129**: 457-464.

Western Regional Climate Center. 2011. Retrieved from http://www.wrcc.dri.edu/climatedata/comparative/

Wright, I.J. and Westoby, M. (1999). Differences in seedling growth behavior among species: trait correlations across species, and traits shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **81**: 85-97.

Zald, H.S.J. (2009). Extent and spatial patterns of grass bald land cover change (1948-2000), Oregon Coast Range, USA. *Plant Ecology* **201**:517-529.

Zeevart, Jan A. D. (1962). Physiology of flowering: flowering is hormonally controlled, but the nature of hormones remains to be elucidated. *Science* **137**: 723-731.

Zobel, D.B. and Antos, J.A. (1987). Composition of rhizomes of forest herbaceous plants in relation to morphology, ecology, and burial by tephra. *Botanical Gazette* **148**: 490-500.

APPENDICES

APPENDIX A: Figures

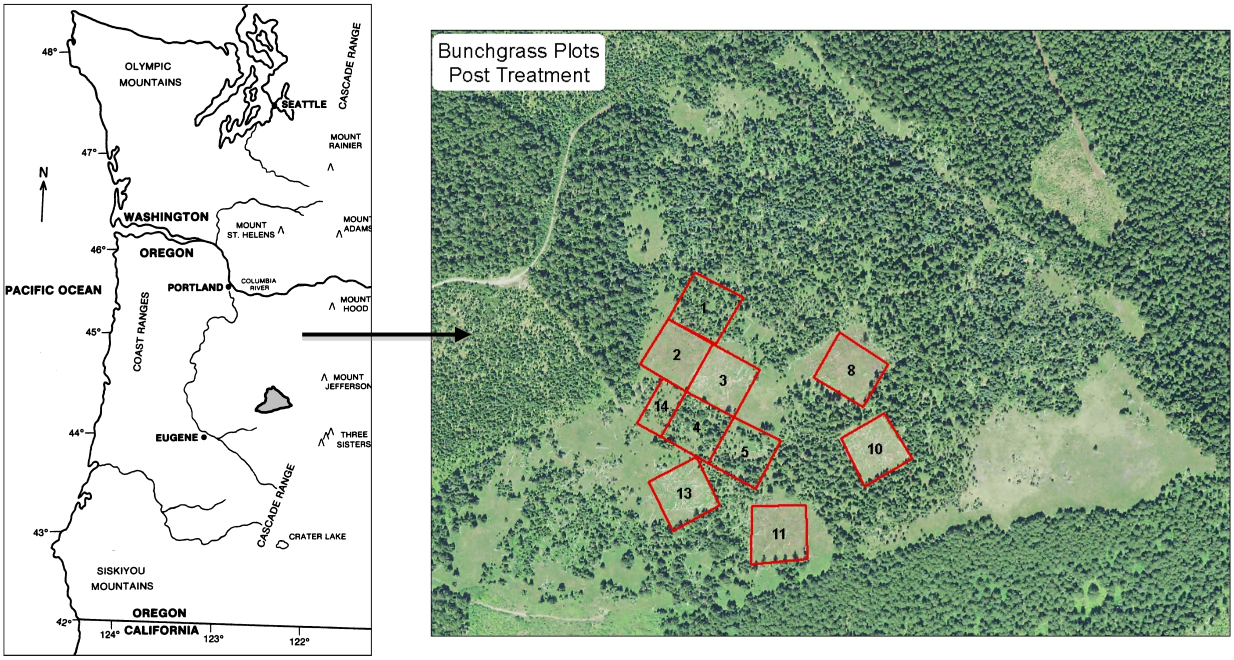

Figure A1. Location of Bunchgrass Ridge on the western slope of the High Cascades in Oregon. The aerial photograph (2010) shows the layout of experimental restoration plots (including controls where we sampled individuals for trait measurement) within the larger mosaic of conifer-invaded meadows.

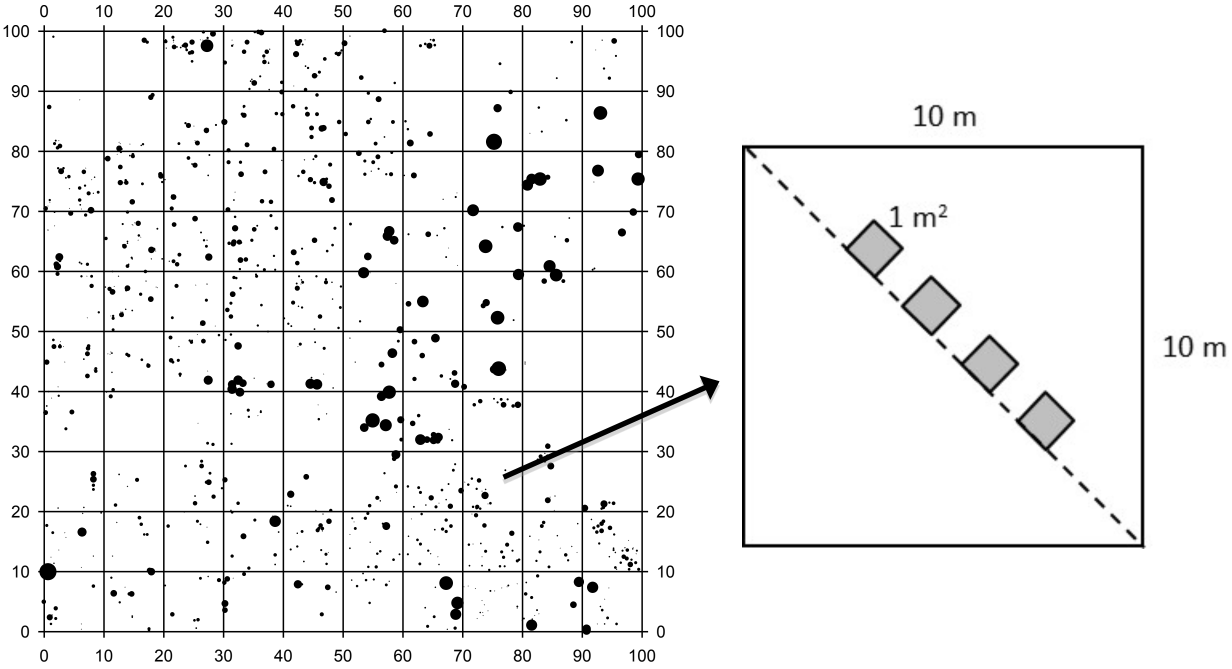

Figure A2. Stem map of one of the 1-ha experimental plots at Bunchgrass Ridge (located on the western slope of the High Cascades of Oregon) showing the mosaic of encroachment states; trees are scaled by diameter (from Haugo and Halpern 2007). Each plot contains 100, 10 m × 10 m subplots; subplots are sampled with four, 1 m^2 quadrats. Quadrats were used to estimate cover (%) of individual meadow species in 2003 and 2014. Light availability (% total transmitted light) was quantified from hemispherical photographs taken either at the centers of subplots (2003) or above each quadrat (2014).

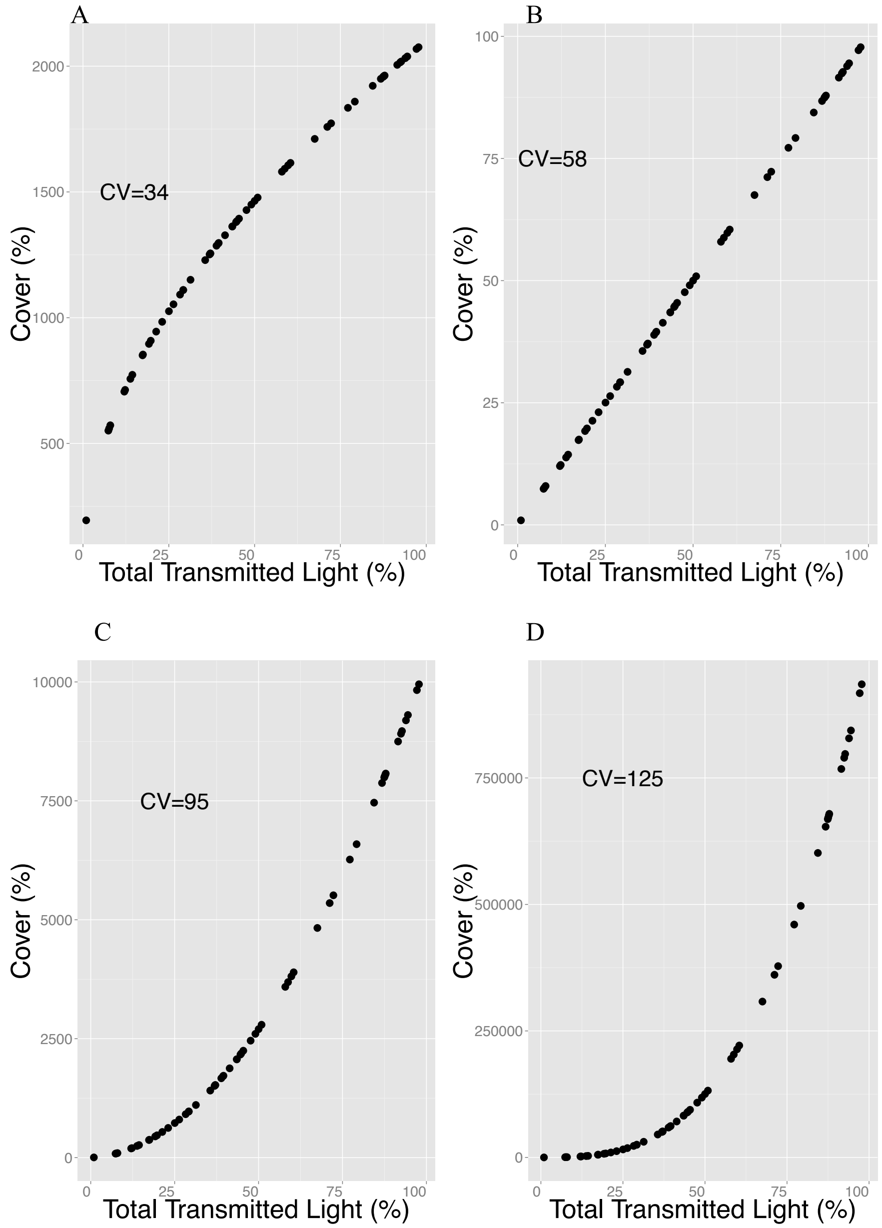

Figure A3. Simulated cover-light relationships and their corresponding coefficients of variation (CV; standard deviation divided by the mean). CVs increase from quadratic (A) to linear (B) to exponential relationships (panels C and D).

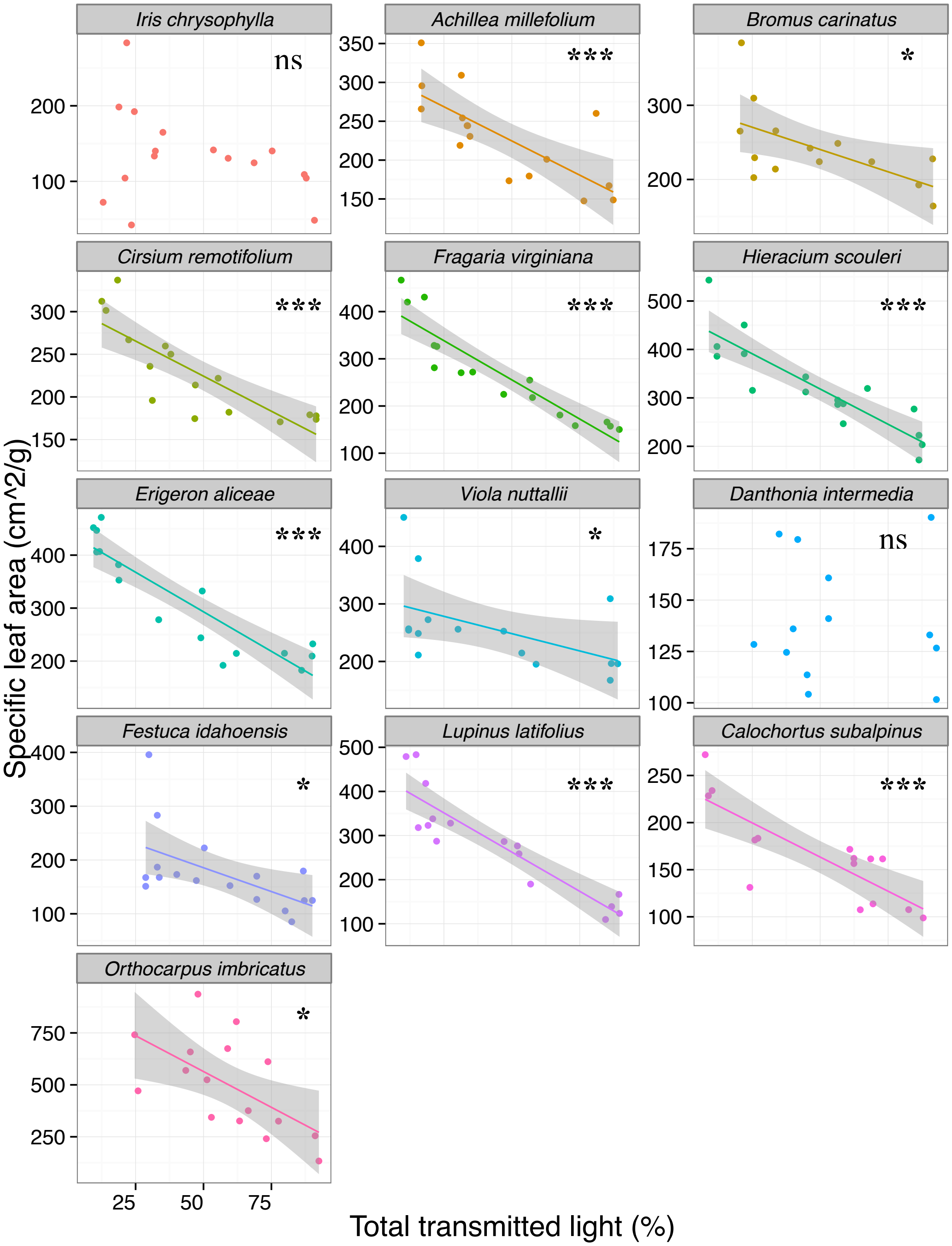

Figure A4. Linear regression models of relationships between specific leaf area (SLA; fresh leaf area divided by dry leaf mass) and light. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in SLA across the light gradient rather differences among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

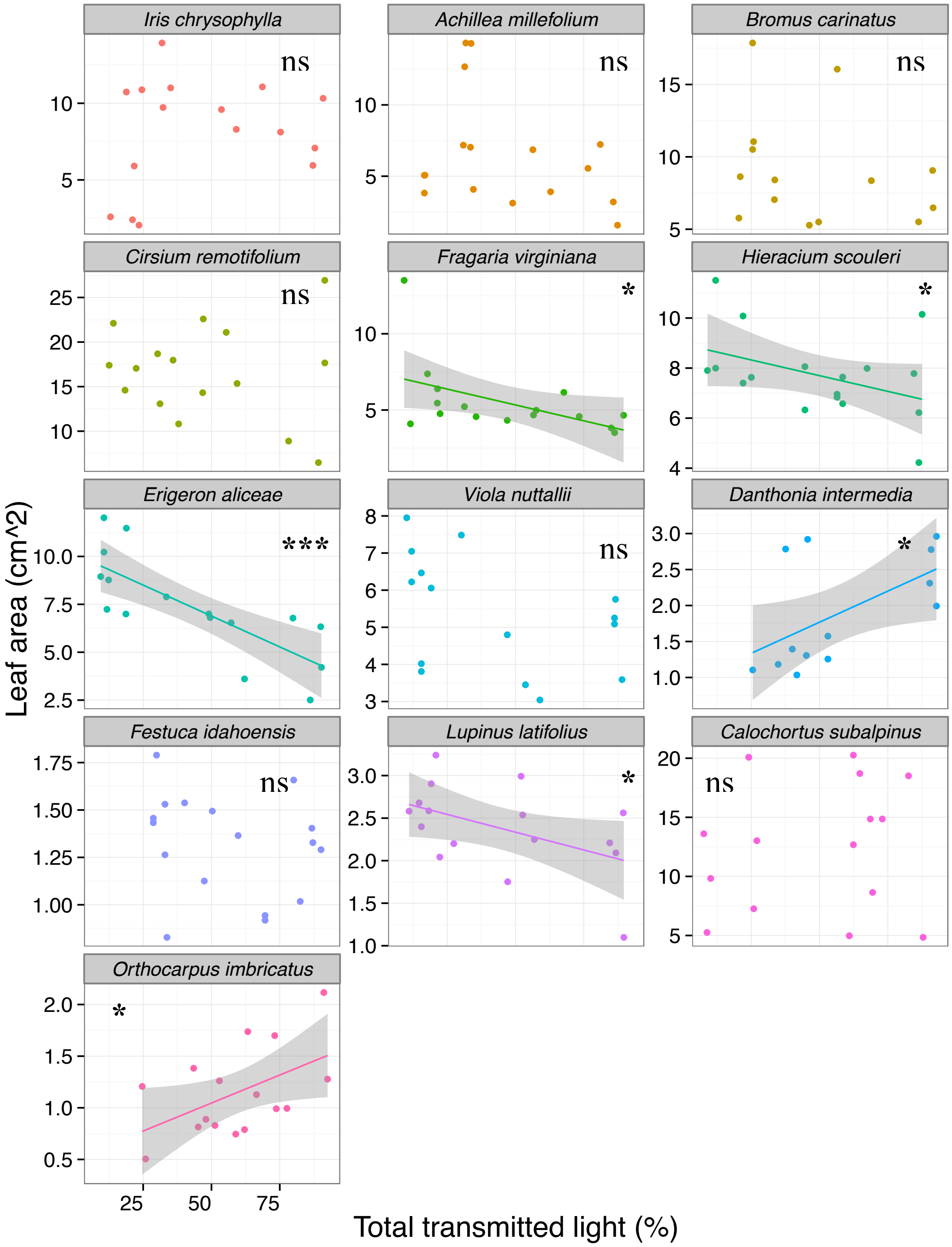

Figure A5: Linear regression models of relationships between leaf area and light. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in leaf area across the light gradient rather differences among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

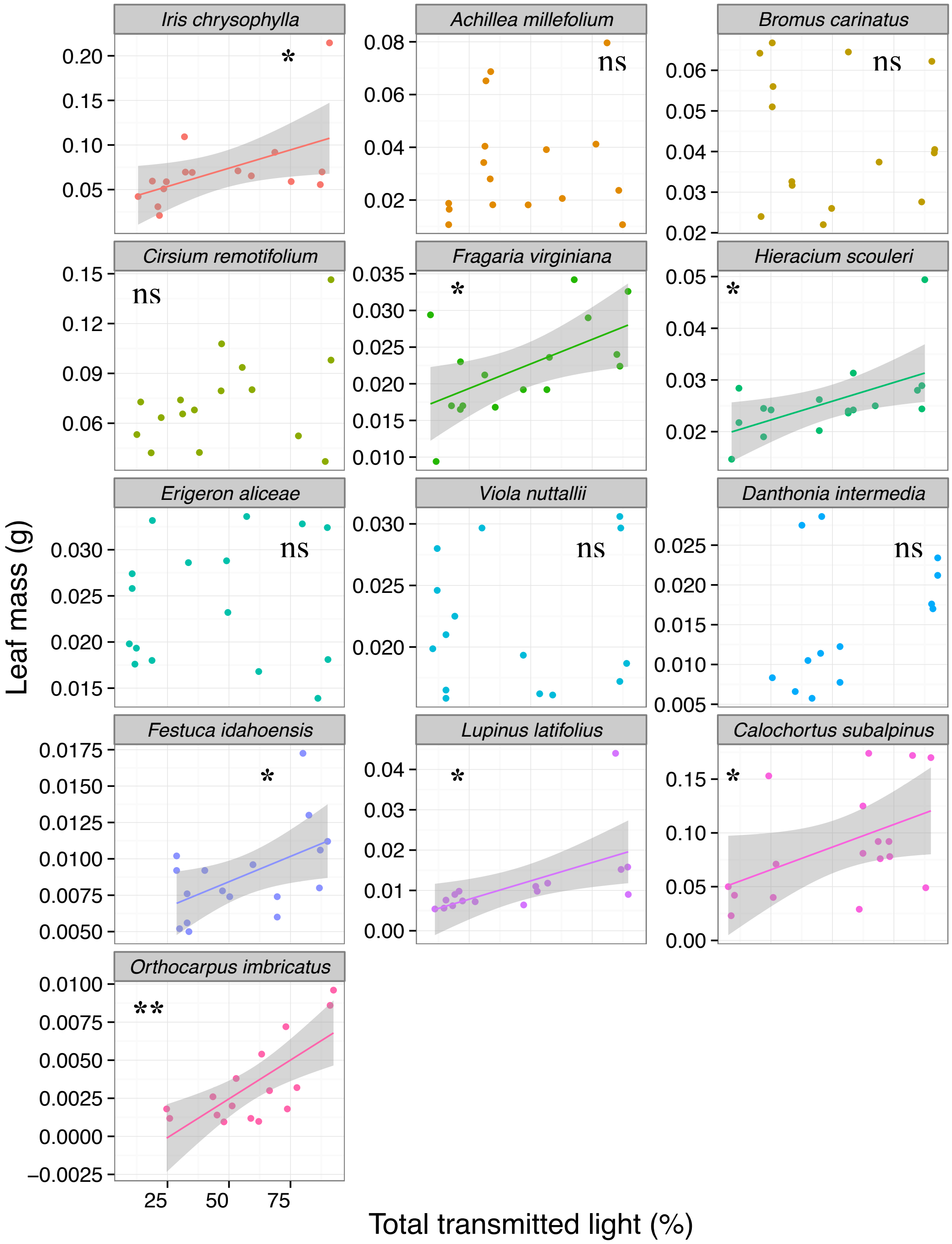

Figure A6: Linear regression models of relationships between leaf mass and light. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in leaf mass across the light gradient rather differences among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

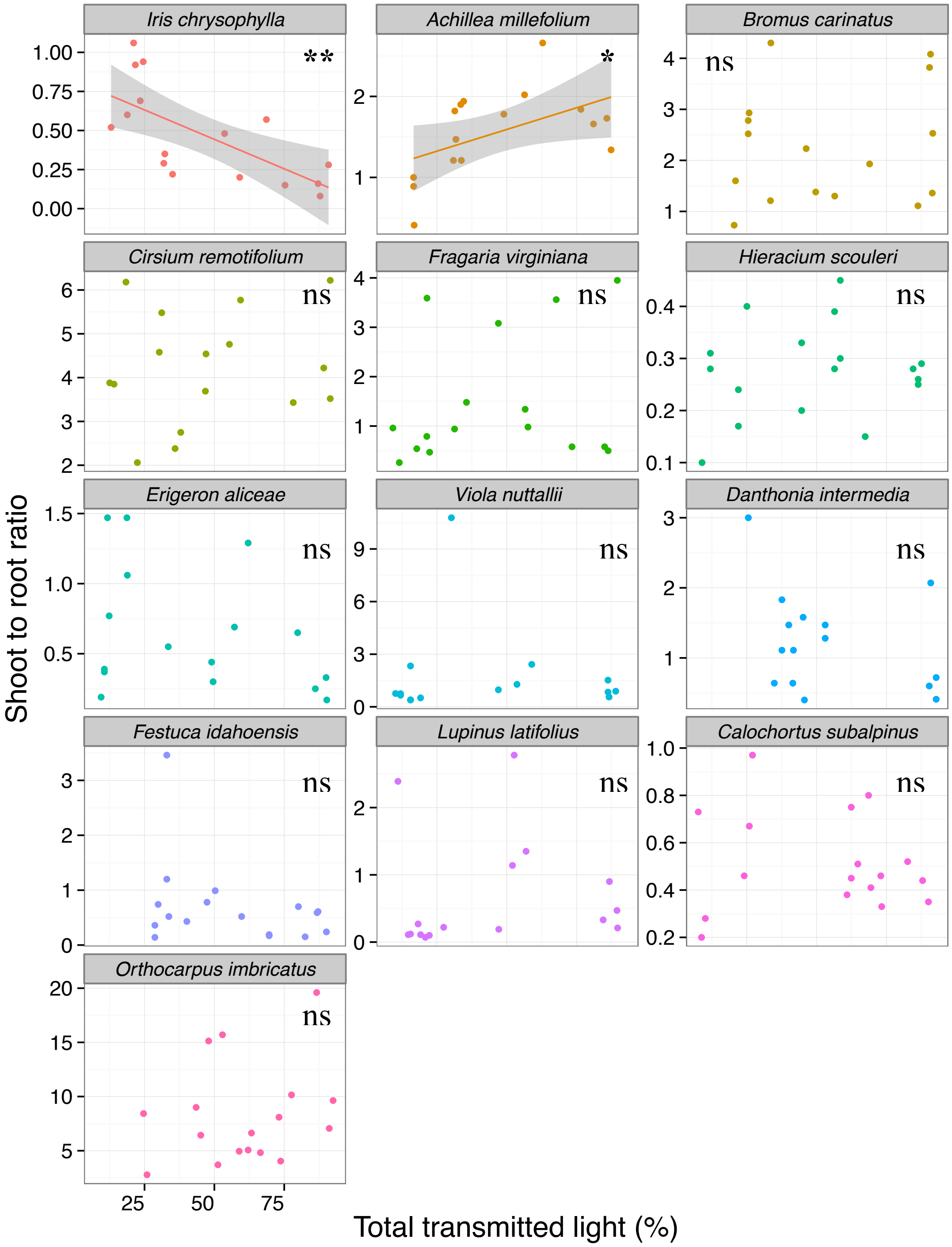

Figure A7. Shoot to root ratio-light relationships based on linear regression models (reproductive biomass not included in ratio). Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in S/R across the light gradient rather differences in S/R among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

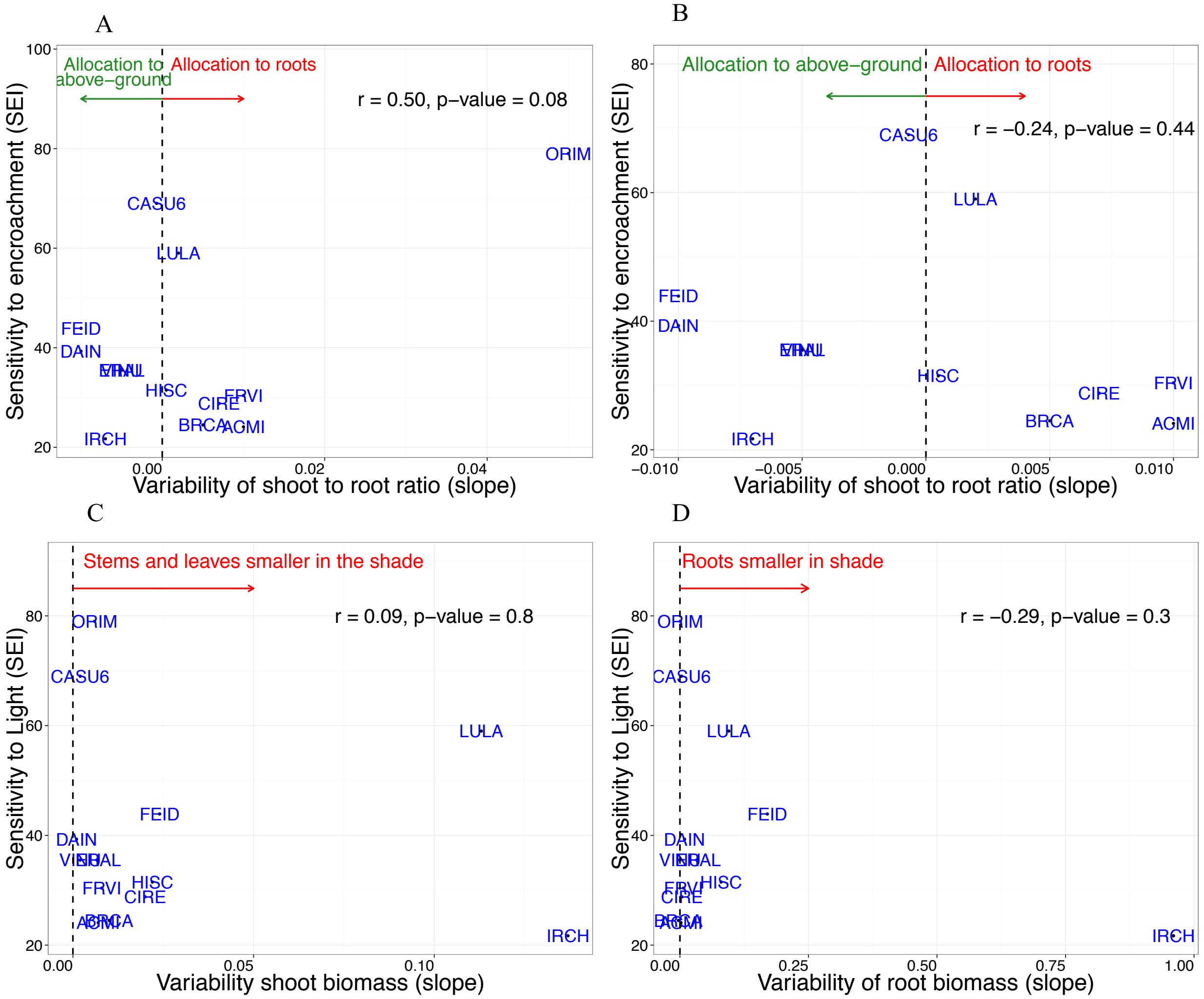

Figure A8. Relationships between variability in biomass traits (slope of the trait-light relationship) and sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship). Species names are in Appendix Table A1 and A2. Dashed vertical line indicates no variation in a trait across the light gradient (zero slope); negative values represent adaptive responses to shading. Relationships are shown for (A) Shoot to root ratio (S/R), all species included; (B) S/R, *Orthocarpus imbricatus* (ORIM) excluded; (C) shoot biomass (shoots and leaves), all species included, and (D) root biomass, all species included.

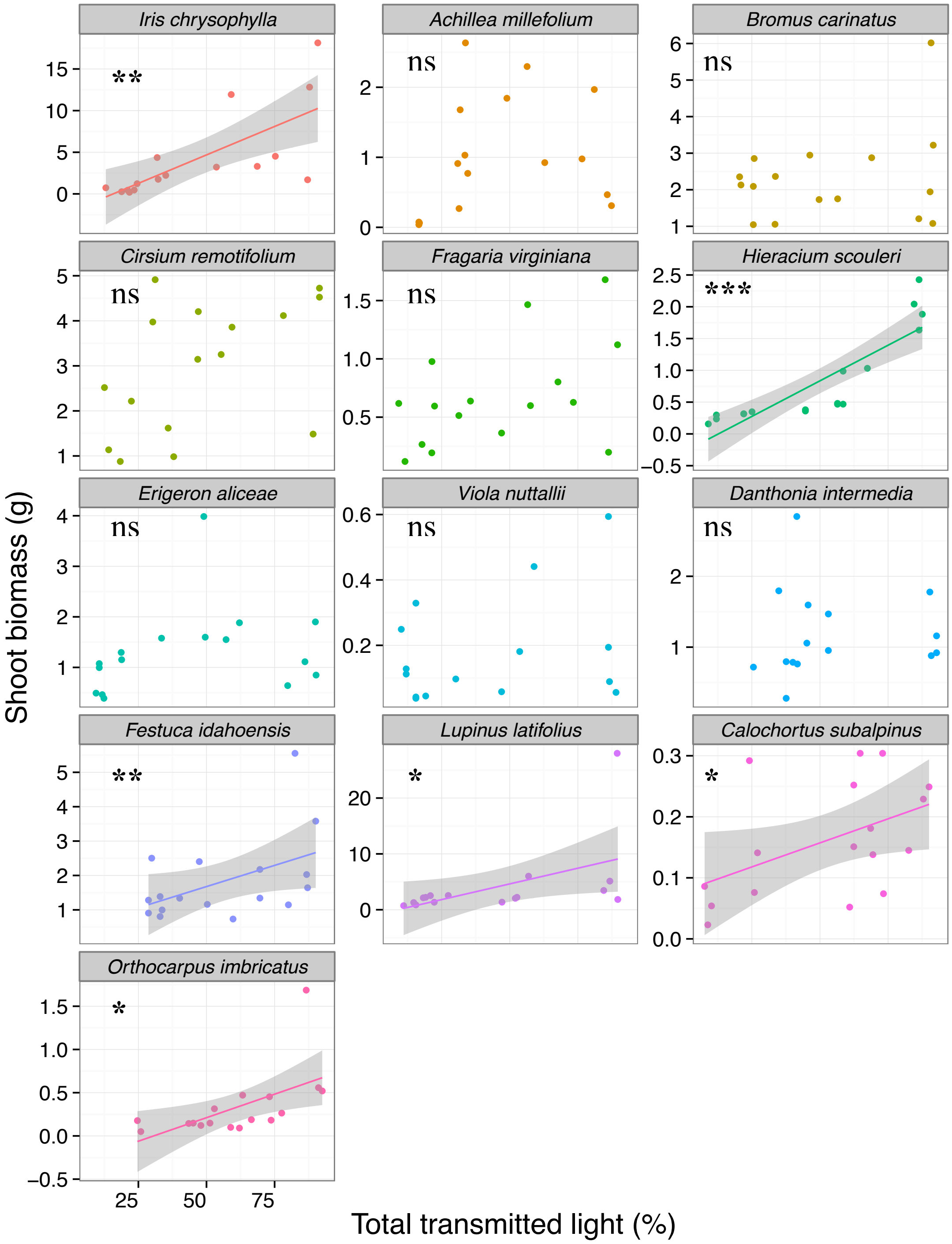

Figure A9. Shoot biomass (includes shoots and leaves, excludes reproductive biomass, S)-light relationships based on linear regression models. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). SEI is the CV of predicted means across the light gradient (see *Data analyses*). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in S across the light gradient rather differences in S among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

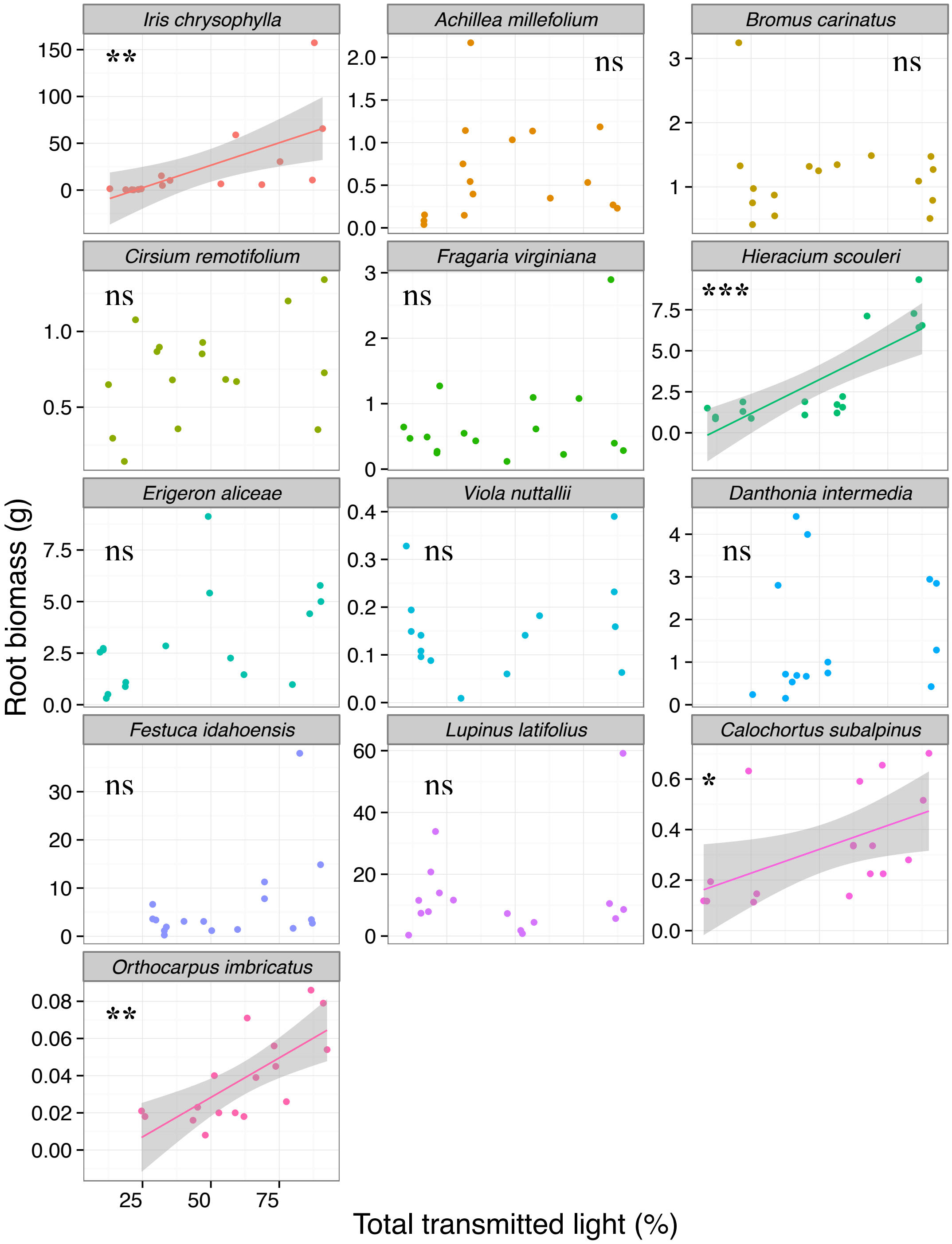

Figure A10. Root biomass (R)-light relationships based on linear regression models. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in R across the light gradient rather differences in R among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

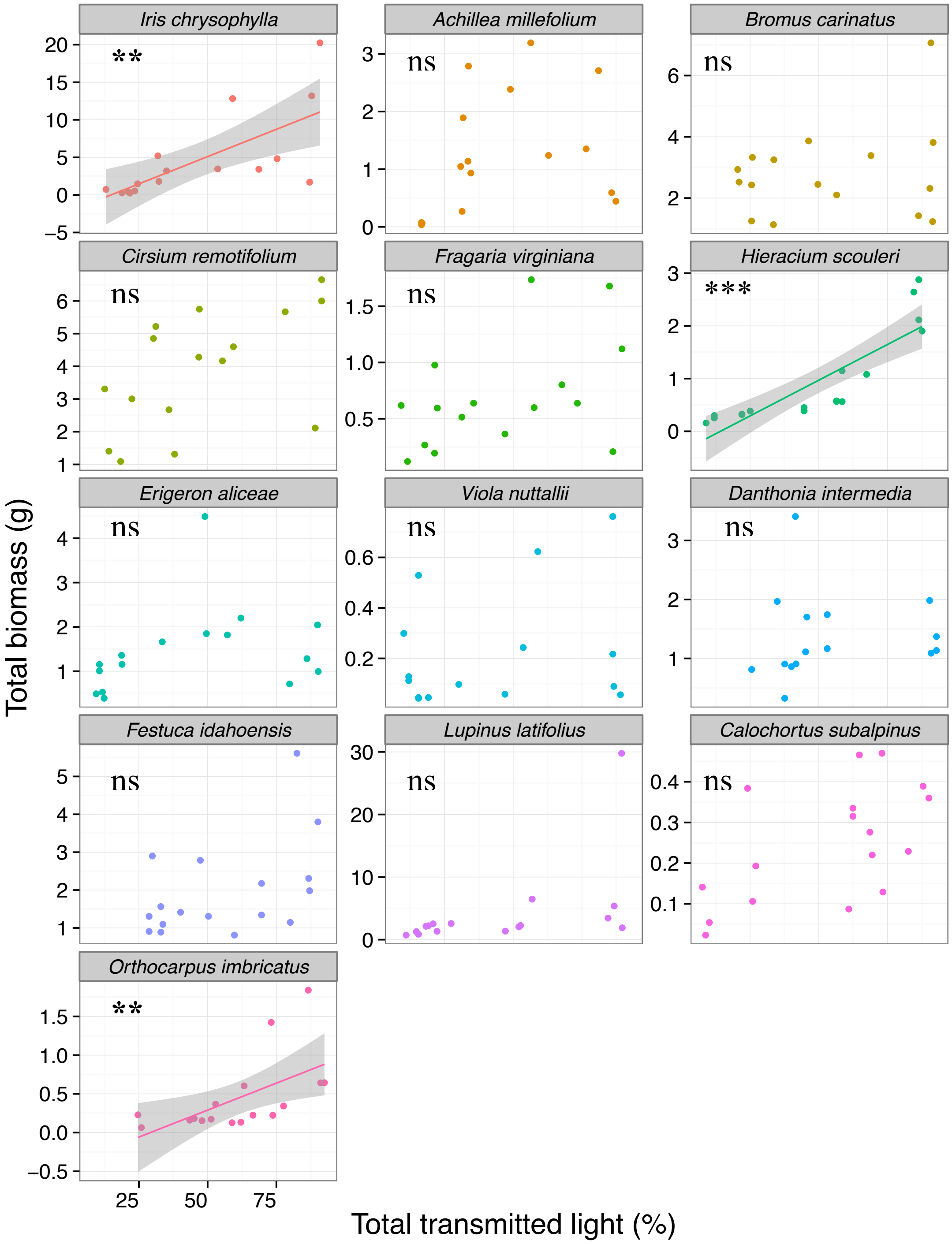

Figure A11. Total biomass-light relationships based on linear regression models. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in total biomass across the light gradient rather differences among species. Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

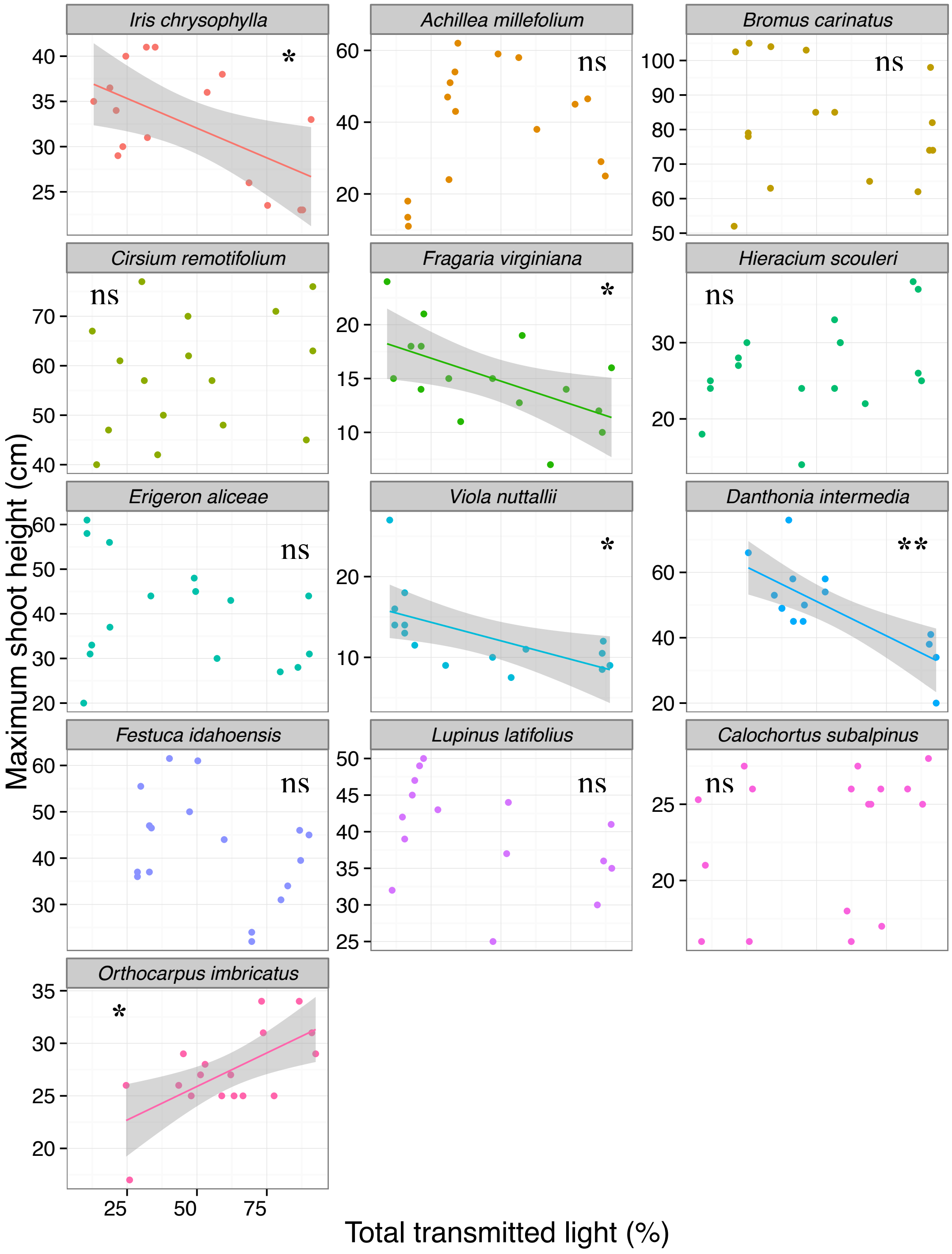

Figure A12. Maximum shoot height -light relationships based on linear regression models. Species are ordered by sensitivity to encroachment (SEI; coefficient of variation [CV] from predicted values of the cover-light relationship, low to high). Gray bands represent confidence intervals. Trait value scales vary to emphasize changes in SH across the light gradient rather differences in SH among species.
Significance is coded as: ns=non-significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

APPENDIX A: Table

Table A1. Mean cover and standard deviation (SD) of species among subplots in which they were present and their corresponding sensitivities to encroachment (SEI), derived from the coefficient of variation (CV; standard deviation divided by the mean) of predicted values of cover across the range of light values sampled. Species are ordered from least to most sensitive to light.

Species	**Code**	***n***	**Cover (%)**	**SD**	**SEI (CV)**	**Light Range (%)**
Iris chrysophylla	IRCH	316	2.8	3.8	22	8.1 – 93.4
Achillea millefolium	ACMI	409	3.3	3.6	24	6.9 – 93.4
Bromus carinatus	BRCA	169	5.5	6.1	25	8.4 – 88.3
Cirsium remotifolium	CIRE	307	3.0	3.7	29	6.9 – 93.4
Fragaria virginiana	FRVI	57	5.8	9.0	30	10.2 – 93.4
Hieracium scouleri	HISC	174	3.4	3.9	32	8.1 – 90.4
Erigeron aliaceae	ERAL	352	3.7	4.1	36	7.1 – 93.4
Viola nuttallii	VINU	166	0.3	0.4	36	8.1 – 93.4
Danthonia intermedia	DAIN	69	1.6	1.3	39	11.9 – 89.8
Festuca idahoensis	FEID	224	9.5	9.3	44	8.1 – 89.8
Lupinus latifolius	LULA	238	4.7	5.9	59	8.1 – 93.4
Calochortus subalpinus	CASU6	64	0.2	0.5	69	14.4 – 88.9
Orthocarpus imbricatus	ORIM	81	2.8	3.4	79	8.1 – 90.4