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Intraspecific trait variation and the differential decline of meadow species during conifer encroachment

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Abstract Conifer encroachment has reduced the extent and habitat quality of mountain meadows throughout western North America. Past studies in the Cascade Range of Oregon reveal surprising variation in the pace at which meadow species are lost to encroachment. We hypothesized that this variation relates to intraspecific variability in plant functional traits that are adaptive as light levels decline during the transition from open meadow to closed forest. For 13 meadow species with varying sensitivities to encroachment, we compared how the rate of decline in abundance relates to intraspecific variation in three morphological traits (specific leaf area, shoot/root ratio, and shoot height) and to clonal ability (no, limited, or strong potential for vegetative spread). For each species, we computed an index of sensitivity to encroachment, ISE, the coefficient of variation in cover across the light gradient. For each trait of each species, we computed an index of variation, the linear slope of the relationship between trait values and available light. For most traits, the correlation between ISE and trait variation (or clonality) was weak. Although specific leaf area increased in the shade for all species, the magnitude of increase did not correlate with ISE. Only variability in leaf area was positively correlated with ISE, increasing in the shade for less sensitive species and decreasing for more sensitive species. Responses to encroachment may reflect differences in species' physiological rather than morphological variability, or species may be responding to changes in resources other than, or in addition to, light.

Keywords Intraspecific variability · Plant morphological traits · Specific leaf area · Light availability · Meadows · Conifer encroachment

Introduction

Invasion of grasslands by woody plants is occurring globally (Archer et al. 1995; Scholes and Archer 1997; Briggs et al. 2005; Highland and Jones 2014). In the western Cascade and Coast Ranges of Oregon, conifer encroachment has reduced the extent of mountain

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meadows by as much as 50% since the mid-1940s (Dailey 2007; Takaoka and Swanson 2008; Zald 2009). Many factors have contributed to encroachment and meadow loss in this region, including cessation of sheep grazing, fire suppression, changes in climate, and positive feedbacks among invading trees (Vale 1981; Miller and Halpern 1998; Halpern et al. 2010; Rice et al. 2012). Although species' loss is an inevitable consequence of encroachment, meadow forbs and grasses vary in the rates at which they are eliminated (Haugo and Halpern 2007). Some species show rapid declines after trees establish, whereas others can persist in the understory for decades. Here, we ask whether interspecific differences in survival can be explained by intraspecific variation in functional traits that determine the range of physical or biotic environments that species can occupy. Chronosequence-based studies of these meadows demonstrate a strong negative relationship between duration of tree influence (decades to over a century) and light availability on the forest floor (Haugo and Halpern 2007). Therefore, we focus on four morphological traits related to the interception of light, the resource assumed to be most limiting as meadow is replaced by forest: specific leaf area (SLA; ratio of leaf area to leaf mass), biomass allocation to above- versus below-ground structures (shoot/root ratio, or *S*/*R*), shoot height, and clonality (no, limited, or strong potential for vegetative spread).

Plant functional traits include morphological, physiological, or life-history attributes that contribute to growth and survival, and thus determine the spatial and temporal distributions of species (Reich et al. 1997; Cingolani et al. 2007; Osnas et al. 2013). Comparative studies of species' distributions often focus on interspecific (Petchey and Gaston 2006; Cornwell and Ackerly 2009; Messier et al. 2010; Castro-Diez 2012), rather than intraspecific, variation in these traits (Laurans et al. 2012; Violle et al. 2012; Gianoli and Saldaña 2013). Nevertheless, differences in intraspecific variability of traits can explain differences in species' niche breadth or environmental tolerance (McAlpine and Jesson 2007; Suding et al. 2008; Jung et al. 2010; Gianoli et al. 2012). For example, in temperate forests of Chile, shade tolerance is correlated with species' ability to adjust SLA and leaf size (Saldaña et al. 2005; Gianoli and Saldaña 2013). An increase in SLA in response to shading allows greater light capture for a given investment in leaf mass (Ackerly and Cornwell 2007) and aids in maintaining a positive carbon balance as light becomes limiting. Similarly, variability in SLA correlates with niche breadth in heathland species along a light gradient from open peat bog to closed forest (Burns 2004).

Plants can also adjust to changes in resource availability by shifting biomass allocation within and among resource-acquiring organs. Optimal partitioning theory predicts that plants should allocate biomass to the organ that acquires the most limiting resource (Bloom et al. 1985; Tilman 1988; Gedroc et al. 1996). This prediction is supported by studies in which biomass allocation shifts from below- to above-ground organs under declining levels of light (Walters et al. 1993; McConnaughay and Coleman 1999; Poorter 2001) and, conversely, to below-ground organs when nutrients are more limiting (Poorter and Nagel 2000). In addition to altering biomass allocation, plants can modify their growth forms in ways that enhance resource capture. For example, they can produce elongated shoots in the shade, thus escaping light interception by neighbors (Hirose and Werger 1995; Schmitt et al. 1995). Finally, species vary in clonal potential—the ability to spread laterally via rhizomes, stolons, or tillers—thus, the ability to access resources in neighboring environments (van Groenendael and de Kroon 1990; de Kroon and Hutchings 1995; Stueffer et al. 1996; Louâpre et al. 2012). In resource-rich environments clonal species tend to develop shorter internodes between ramets, whereas in resource-limited environments (e.g., low light), they can develop longer internodes, increasing the likelihood of encountering patches of greater resource availability (Dong 1993; Svensson et al. 1994). In contrast, non-clonal species are unable to spread laterally to take advantage of local resource heterogeneity.

In this study, we explore whether the differential decline of meadow species during conifer encroachment is correlated with intraspecific variation in morphological traits related to light interception. We hypothesized that species that are more sensitive to encroachment would show less variation in morphological traits related to light capture than would species that are less sensitive to encroachment. Specifically, we hypothesized that as light declined, more sensitive species would show smaller increases in SLA, allocation to shoots, and shoot height. Similarly, we hypothesized that species with no or limited clonal potential would be more sensitive to light than would species with strong clonal potential.

Materials and methods

Study site

Bunchgrass Ridge forms a gently sloping plateau 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). The climate is characterized by cool, wet winters and warm, dry summers. Temperatures at Santiam Pass (~1467 m elevation), 17 km to the north of Bunchgrass Ridge, average −3.1 °C in January and 17.0 °C in July (Western Regional Climate Center 2015). Annual precipitation is ~216 cm, but it is highly seasonal, with only 7.5% falling between June and August. Total snowfall averages ~11 m and snow can persist until late May or early June.

The 100-ha plateau supports a fine-scale mosaic of open meadows and coniferous forests of varying ages, reflecting two centuries of invasion by *Abies grandis* and *Pinus contorta* (Halpern et al. 2010; Rice et al. 2012). Meadows contain a diversity of graminoids and forbs characteristic of mesic and dry sites in this region (Haugo and Halpern 2007; Halpern et al. 2012; McCain et al. 2014). With encroachment, these species are gradually replaced by shade-tolerant herbs typical of mesic forests (Haugo and Halpern 2007, 2010). Soils are fine sandy loams derived from andesitic basalts and tephra deposits with varying amounts of glacial-derived stones and boulders. Soils range from Vitric Melanocryands in open meadows to Aquic Vitricryands where trees have been present for more than a century (C. Halpern, unpublished data). However, soil profiles across the encroachment gradient indicate that prior to recent tree invasion, grassland had dominated the plateau for centuries, if not millennia (D. Lammers, personal communication). Although one or more extrinsic factors (e.g., changes in climate or disturbance regime) likely triggered these invasions, direct evidence of these changes is lacking. However, spatio-temporal reconstructions of establishment history suggest that once initiated, strong internal feedbacks (tree–tree interactions) have sustained the invasion process (Halpern et al. 2010; Rice et al. 2012).

Measurements of meadow species cover and light

We combined two sets of data from Bunchgrass Ridge to quantify the relationships between meadow species' abundance and light availability across the encroachment gradient. The first set, collected in 2004, comprised pre-treatment data from a large-scale restoration experiment (tree removal with and without fire; Haugo and Halpern 2007; Halpern et al. 2012, 2016). Within each of the nine, 1-ha experimental plots (100 × 100 m) and one 0.5-ha plot (50 × 100 m), a grid system was established to create 100 (or 50) 10 × 10 m subplots. We selected 32–84 subplots per plot (537 in total) to sample the mosaic of encroachment states—from residual meadow openings, to patches of recent (decade-old) invasion, to considerably older forests (>130 year). The second set of data, collected in 2014, comprised 80 subplots from the three untreated (control) plots, or from newly established subplots adjacent to these (to obtain greater representation of open meadow).

Each subplot was sampled with four 1 × 1 m quadrats; these were spaced 1 m apart along the northwest to southeast diagonal. Cover (%) of each meadow species was visually estimated in each quadrat then averaged for the subplot. To estimate available light, a hemispherical photograph was taken ~1 m from the ground surface at the center of each subplot (2004) or above each quadrat (2014) using a Nikon Coolpix p900 digital camera and FC-E8 fisheye converter. Hemispherical images were analyzed using Gap Light Analyzer software (Frazier et al. 1999) to compute light availability over the growing season (April to September), expressed as total transmitted light (i.e., percentage of above-canopy light; 0–100%). Values were averaged for the four quadrats per subplot in 2014 to enable pooling of the two datasets (see "Analyses" section).

Species selection and measurements of plant morphological traits

From the ~70 meadow species present at Bunchgrass Ridge, we chose 13 (10 forbs and three grasses) to represent the range of species' sensitivities to encroachment (Haugo and Halpern 2007). Twelve species are perennial and one is an annual. Nomenclature follows USDA NRCS (2015).

For each species, we selected 15–17 mature individuals (216 in total) using a stratified-random approach to ensure that each species was sampled across the encroachment gradient. Specifically, for each species, 3–5 mature, healthy individuals were randomly chosen from each of four light environments: open meadows distant from forest edge; small residual meadow openings; younger, relatively open forests; and older, closed-canopy forests. Except for the annual, *Orthocarpus imbricatus*, most individuals selected likely established in open meadow environments (prior to encroachment) because reproduction from seed is uncommon in the forest understory. Prior to excavation, a hemispherical photograph was taken above each individual to characterize the light environment (as described above).

We measured four morphological traits for each plant (means and ranges of trait values are presented in Online Resource 1). Measurements were made between June 25 and August 5, 2014. First, maximum shoot height (hereafter, shoot height) was measured as the distance from the ground surface to the tip of the tallest leaf. Each plant was then excavated. From the chosen 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). Each plant component (shoots, leaves, reproductive tissues, and root systems) was bagged separately and transported to the lab. Root systems were carefully washed to remove soil. All plant components were dried at 60 °C for 48 h or until weights stabilized. Fresh leaf area and dry leaf mass (from which SLA was determined) were measured on one to five healthy, mature leaves per individual, then averaged for each individual. Leaf area was estimated using ImageJ 1.48v software (Rasband 2014) from fresh leaves that were pressed and photographed in the field. Ratio of above- to below-ground mass (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 (i.e., rhizomes, bulbs, and roots). Because reproductive phenology differed among species, reproductive tissues, if present, were not included in S/R.

Clonality was treated as an ordinal trait. Species were assigned to one of the three classes based on field observations and descriptions from regional floras (Hitchcock and Cronquist 1973; Pojar and MacKinnon 1994; Baldwin et al. 2012): (1) non-clonal, (2) limited clonality (limited lateral spread by tillers, short rhizomes, or branching caudices), or (3) strongly clonal (potential for extensive lateral spread via long rhizomes or stolons).

Analyses

The relationship between species' cover and light was used to develop a novel index of sensitivity to encroachment (ISE). Preliminary species' models indicated that cover–light relationships were similar for the 2004 and 2014 datasets, thus data were combined to increase sample size. For each species, we fit a local polynomial regression model, regressing non-zero cover values (i.e., cover given species' presence) on total transmitted light. Models were run with the *loess* function in the *stats* package of R ver. 3.0.2 (R Core Team 2013). We used a large spline value (0.9) to avoid over fitting the data. This local-modeling approach was conducive to developing a common index among species when the form of the cover–light relationship differed (e.g., exponential decline, linear decline, or initial increase then decline; see Fig. 1). Local models were used to generate predicted values of cover at increments of 0.1% light over the range of light values common to all species (14.5–88.3%). We then computed the coefficient of variation (CV) of predicted cover as the index of sensitivity to encroachment (ISE). A low CV (low variation in cover across the light gradient) corresponded to low sensitivity to light; a high CV (high variation in cover) corresponded to a high sensitivity to light. Simulations of cover–light relationships for a diversity of model forms (exponential, linear, and quadratic) and for models with varying slope parameters confirmed that the CV is a robust index of sensitivity to light. Steep exponential declines in cover (species highly sensitive to changes in light) yielded higher CVs than did linear or quadratic declines (species less sensitive to changes in light). Similarly, steeper linear declines in cover (steeper slopes) yielded higher CVs than did shallower declines (Celis 2015).

We quantified trait variation, i.e., variability in SLA, S/R, and shoot height, as the linear slope of the trait–light relationship ($n = 15$–17 individuals per species). In contrast to the cover–light relationship, we used the slope to quantify trait variation because it

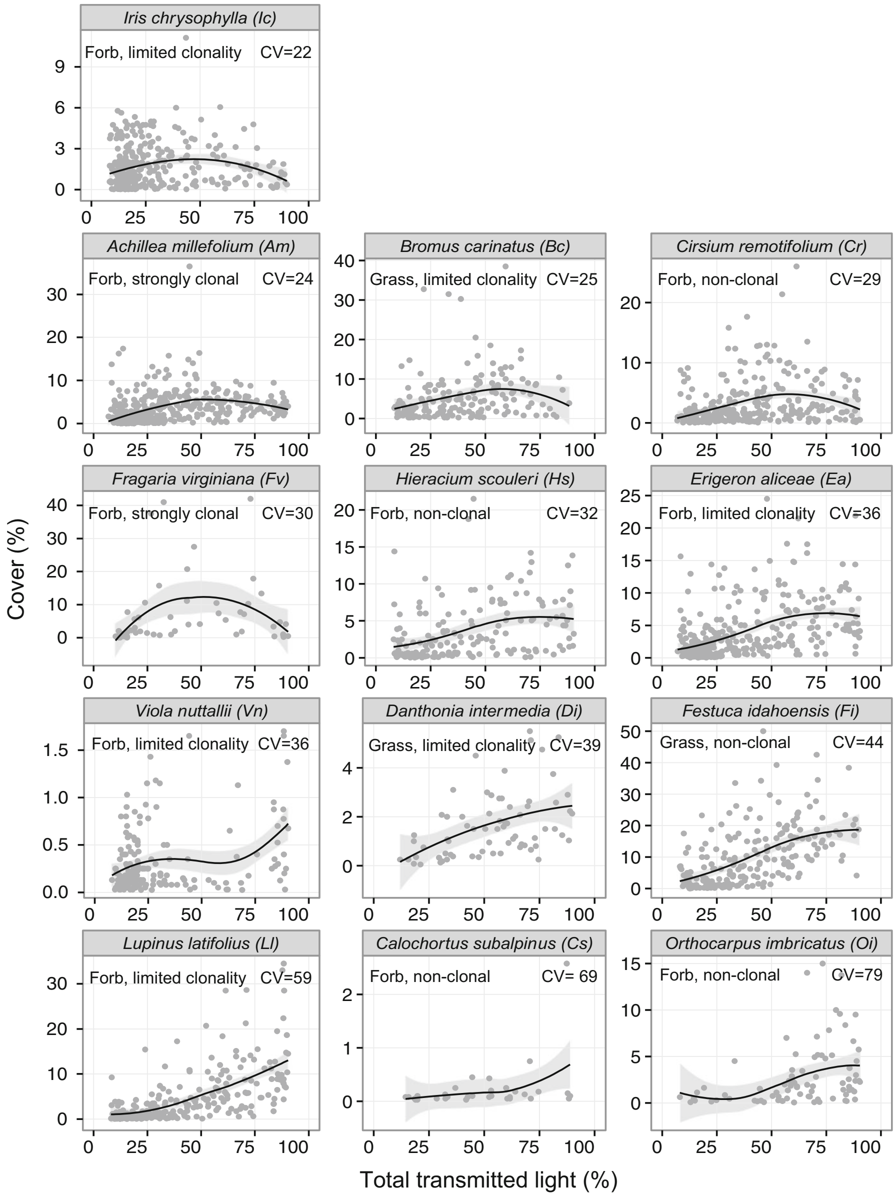

Fig. 1 Species' cover–light relationships based on local polynomial regression models. *Gray bands* are confidence intervals. The index of sensitivity to encroachment, ISE, is computed as the coefficient of variation (CV) of predicted cover across the light gradient (see Materials and methods and Analyses sections). Species are ordered by increasing ISE (*left* to *right*, *top* to *bottom*). The scale of the *Y* axis varies among species to highlight changes in cover across the light gradient rather than differences among species. All species are perennial except for the annual, *Orthocarpus imbricatus*

captures both the magnitude of change across the light gradient and its sign (positive or negative), which differed among species and traits. In this way we could distinguish between responses that were potentially adaptive (e.g., an increase in SLA or *S*/*R* with a reduction in light) and those that might be indicative of stress or resource limitation (e.g., a decrease in shoot height). To aid in interpretation of the ratio-based traits (SLA and *S*/*R*), we also modeled the relationship with light for each component of each trait: leaf area and leaf mass for SLA, and shoot mass and root-system mass for *S*/*R*. Linear models were developed using the *lm* function in the *stats* package of R ver. 3.0.2 (R Core Team 2013). Although our indices of sensitivity to encroachment (ISE) and trait variation are based on the relationship between current light availability and plant performance, the strong relationship between light and forest age (Haugo and Halpern 2007) and the fact that most meadow species established prior to encroachment suggest that they are reasonable proxies for the cumulative influence of trees on the light environment. In essence, plants growing in shadier locations have also had a longer history in the shade.

For each quantitative trait, we used Pearson correlation ($n = 13$ species) to test the hypothesized relationship between ISE and trait variation (slope of the linear regression of trait values on light). In addition, to assess whether differences in sensitivity to light relate to inherent differences in trait expression among species, we tested whether ISE was correlated with mean SLA, *S*/*R*, and shoot height. All correlations with mean trait values were non-significant, thus we do not discuss these further. For clonal potential, we conducted a one-way ANOVA testing for a difference in the mean ISE of species representing each clonal group (none, limited, and strong; $n = 2$–6 species per group). Analyses were conducted in the *stats* package of R ver. 3.0.2 (R Core Team 2013).

Results

Species' sensitivity to encroachment (light)

Among the full set of samples (subplots), total light transmittance (% of available light) ranged from 7.1 to 94.3%. The range of species' cover values also varied widely (0.1 to >40%), as did the relationships between cover and light (Fig. 1). Among species, ISE varied more than threefold (range of CV of 22–79; Fig. 1). Among the least sensitive species (*Iris chrysophylla*, *Achillea millefolium,* and *Bromus carinatus*) cover changed little over the light gradient. Among the most sensitive species (*Lupinus latifolius, Calochortus subalpinus*, and *Orthocarpus imbricatus*), cover declined steeply to low levels in the shadiest environments (Fig. 1).

Relationships between sensitivity to light (ISE) and variability in morphological traits

We found little support for the hypothesis that ISE is correlated with intraspecific variation in morphological traits that are potentially adaptive to light interception. Among the 13 species, ISE was not correlated with variation in SLA ($r = -0.44, p = 0.14$; Fig. 2a). Excluding one outlier (annual *O. imbricatus*) reversed the sign of the relationship in the hypothesized direction (steeper increase in SLA in the shade for less sensitive species), but it remained non-significant ($r = 0.24$, $p = 0.46$; Fig. 2a). As expected, SLA increased as light declined for nearly all species (Fig. 3; Online Resource 2), but the magnitude of change (slope of the SLA–light relationship) did not correlate with ISE (Fig. 2a).

Relationships of ISE to variation in leaf area and leaf mass offer insight into the lack of a relationship with SLA. ISE was correlated with variability in leaf area ($r = 0.56, p = 0.05$; Fig. 2b). Leaf area tended to increase in the shade for less sensitive species, but changed little or declined in the shade for more sensitive species (Fig. 2b; see also Online Resources 2, 3). In contrast, ISE was not correlated with variability in leaf mass, which was comparably low among most species ($r = 0.17$, $p = 0.6$; Fig. 2c; see also Online Resources 2 and 4).

Shoot/root ratio (*S*/*R*) varied significantly with light in only two species (Fig. 4; Online Resource 5), thus we did not test the correlation between ISE and variation in *S*/*R*. In most species, shoot and root mass declined in parallel across the gradient, or showed no change with declining light levels (Online Resources 5–7). For the two species in which *S*/*R* varied across the light gradient, allocation to shoots increased in the shade for *I. chrysophylla*, but decreased for *A. millefolium* (Fig. 4; Online Resource 5).

Species showed substantial variation in shoot height with reductions in light. Some species produced etiolated shoots, other species produced shorter shoots, and some species showed no consistent response to shading (Fig. 5; Online Resource 5). Nevertheless, variation in shoot height did not correlate with ISE ($r = 0.13$, $p = 0.70$). Finally, ISE tended to decline from non-clonal to strongly clonal species, but the trend was not significant ($F = 1.66$, $p = 0.24$) due to the large variation within groups (Fig. 6).

Discussion

Montane meadow forbs and grasses in the Cascade Range can vary markedly in their responses to conifer encroachment (Haugo and Halpern 2007). Although some species' populations decline rapidly after tree establishment, others decline more gradually. We hypothesized that these contrasting responses to encroachment were related to differences in intraspecific variability in plant morphological traits

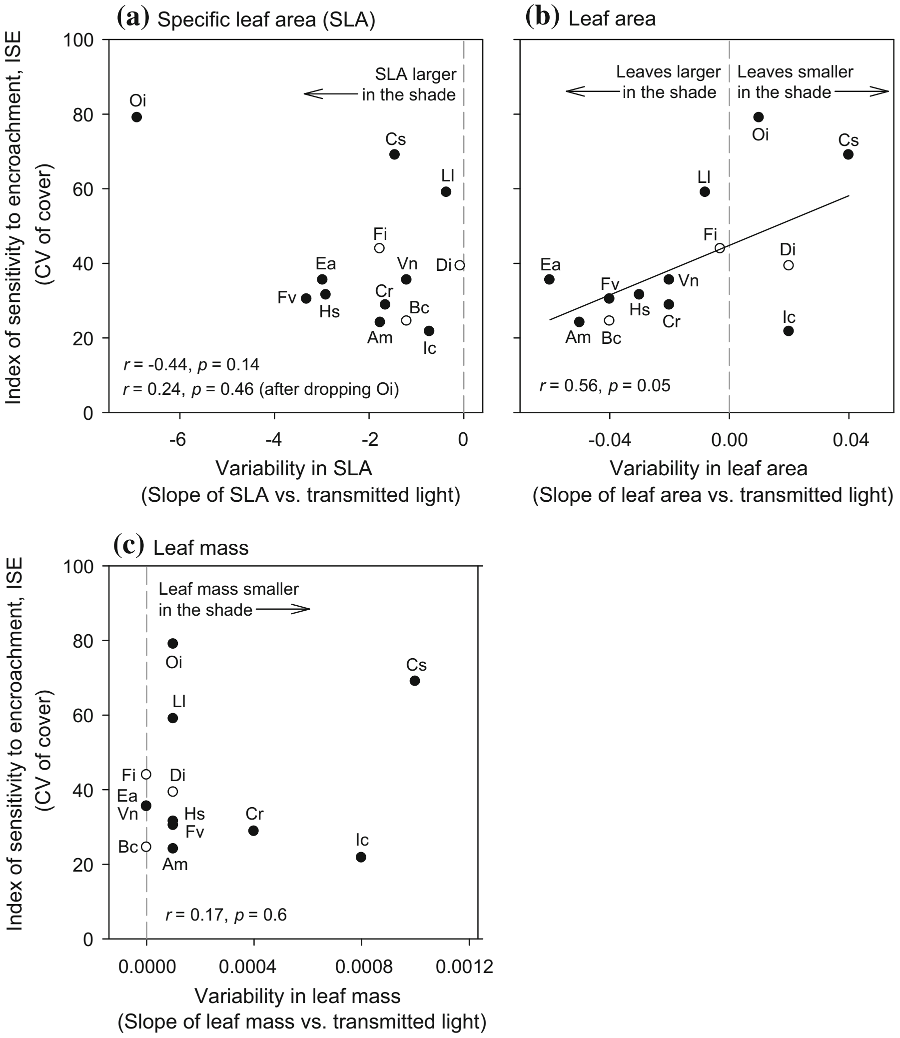

Fig. 2 Relationships between sensitivity to encroachment (ISE) and variability in leaf traits: **a** specific leaf area (SLA; leaf area/leaf mass), **b** leaf area, and **c** leaf mass. Variability in a trait is the linear slope of the trait–light relationship (see see Materials and methods and Analyses sections). Species codes are the first letters of the genus and species (for full names see Fig. 1). *Closed circles* are forbs; *open circles* are grasses. *Dashed vertical lines* at zero indicate no trait variation across the light gradient; *negative values* represent adaptive responses (e.g., increase in SLA or *leaf area in the shade*)

that aid in light capture. However, the results of our analyses offer little evidence that they do. Although for many species, specific leaf area (SLA), biomass allocation (*S*/*R*), and shoot height varied with light availability, the direction or magnitude of this variation did not correlate with sensitivity to light, nor did differences in the mean values of species' traits.

All species showed an increase in SLA with reduced light, a common response to shading (Wright and Westoby 1999; Ackerly et al. 2002; Burns 2004). For a given investment in leaf mass, an increase in leaf area enhances the surface area available for light interception—critical to maintaining a positive carbon balance as light becomes limiting. Nevertheless, the magnitude of response in SLA was not correlated with ISE. Effects on leaf area and leaf mass, the components of SLA, offer some insight into this result. In contrast to the relationship with SLA, ISE correlated significantly with variability in leaf area: less sensitive species developed larger leaves in the shade and more sensitive species developed smaller leaves. At the same time, leaf mass changed minimally or declined.

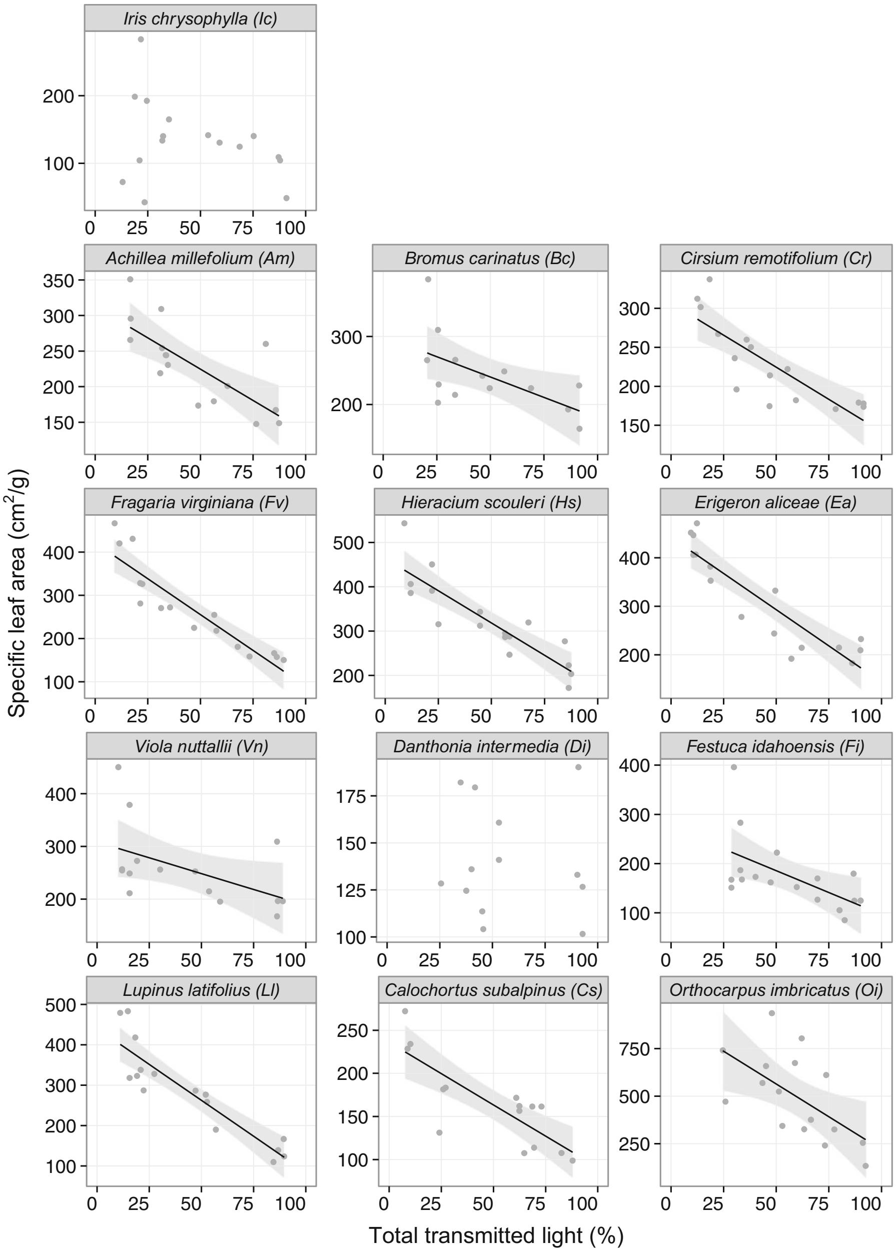

Fig. 3 Relationships between specific leaf area (SLA) and light for the 13 study species. Species are ordered by sensitivity to encroachment (as in Fig. 1). *Gray bands* representing confidence intervals are shown for significant linear relationships. The scale of the *Y* axis varies among species to highlight changes in SLA across the light gradient rather than differences among species. See Online Resource 2 for regression statistics

Thus, for the less sensitive species, changes in leaf form appear adaptive in the shade—increasing in size but decreasing or not changing in mass (Reich et al. 1997; Gianoli et al. 2012; Gianoli and Saldaña 2013). Although more sensitive species may lower metabolic costs by reducing leaf mass, the potential for carbon gain is also reduced by smaller leaf area. In these species, reductions in both leaf area and leaf mass may be symptoms of a negative carbon balance.

Although we focused on the adaptive significance of morphological variability, sensitivity to encroachment may also reflect the ability (or inability) of species to acclimate physiologically to reductions in light. For example, in the shade, some forest understory species can allocate more to light interception and production of chlorophyll *b* than to maintenance of photosynthetic reaction centers and production of chlorophyll *a* (Pearcy and Sims 1994). It is likely that

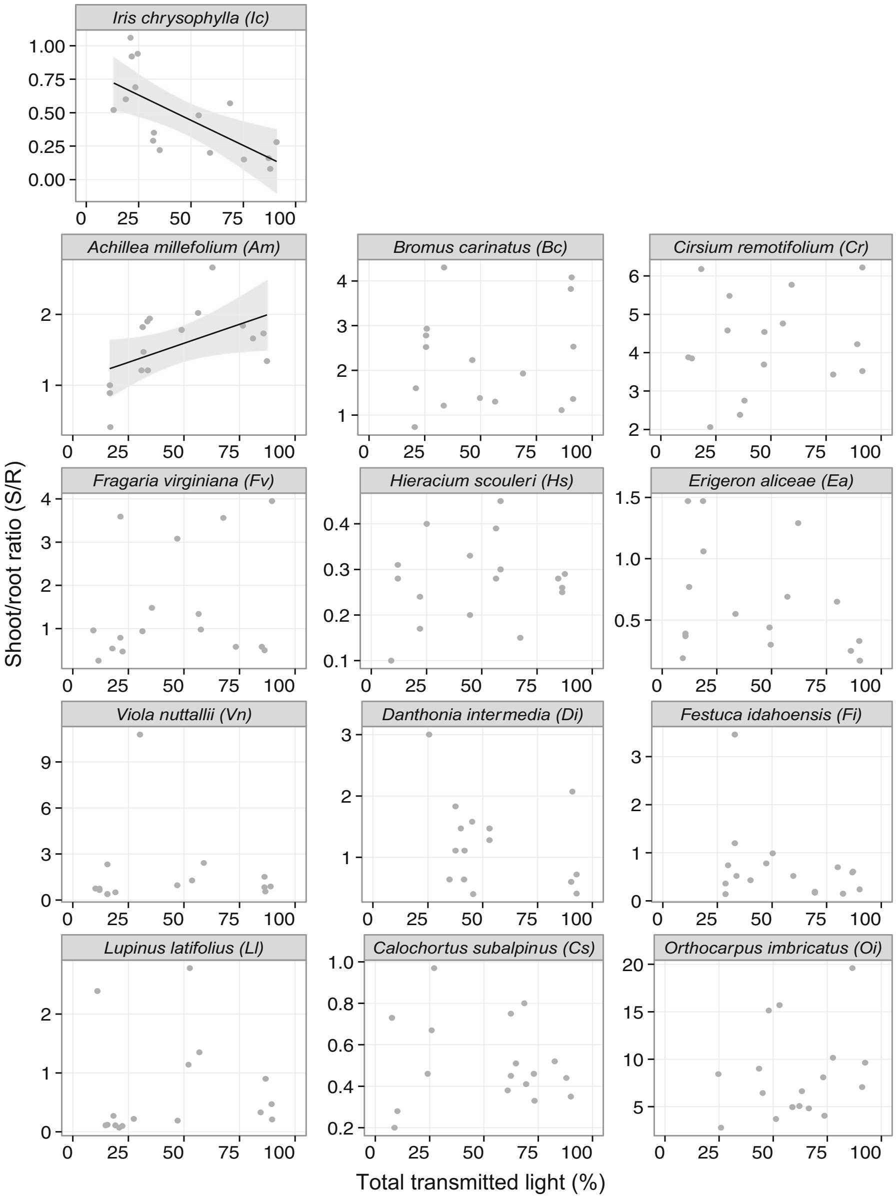

Fig. 4 Relationships between shoot/root ratio (*S*/*R*) and light for the 13 study species. Species are ordered by sensitivity to encroachment (as in Fig. 1). *Gray bands* representing confidence intervals are shown for significant linear relationships. The scale of the *Y* axis varies among species to highlight changes in *S*/*R* across the light gradient rather than differences among species. See Online Resource 5 for regression statistics

similar variation in physiological acclimation to shading exists in meadow species that characterize more open environments.

As with SLA, we hypothesized that sensitivity to encroachment would correlate with the ability to shift allocation of biomass from root systems to shoots and leaves. However, most species showed little change in allocation across the light gradient. Instead, the mass of above- and below-ground structures either declined in parallel or failed to show a significant trend. One plausible explanation is that soil resources, in addition to light, become limiting with the transition from meadow to forest. Plant allocation patterns may thus reflect the outcome of multiple resource limitations and the nature of their interaction (Freschet et al. 2015). In a study of soil properties across conifer-invasion zones at Bunchgrass Ridge, Griffiths et al. (2005) documented reduced nitrogen availability, reduced microbial activity (reflecting changes in litter quality), but increased soil moisture with tree age and density. In the presence of trees, the nature of the below-ground competitive environment is also likely

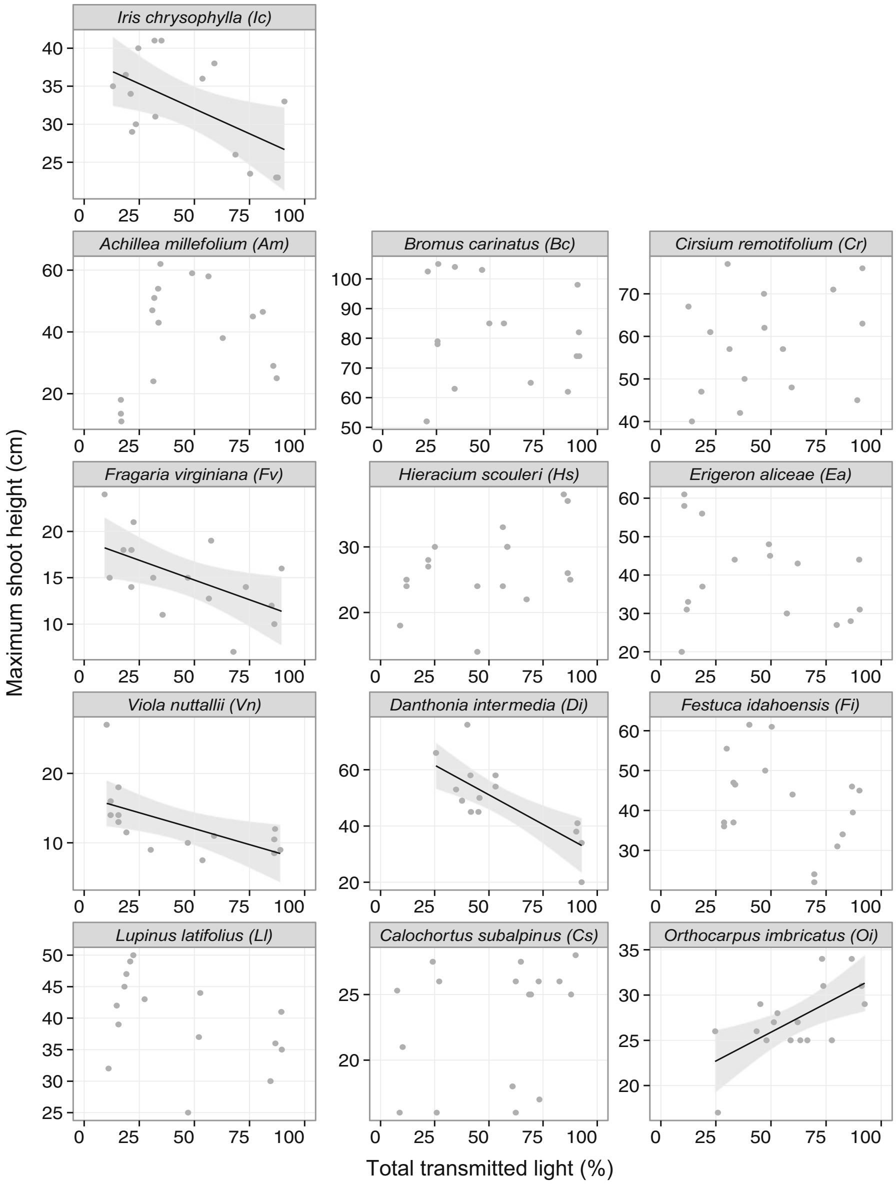

Fig. 5 Relationships between maximum shoot height and light for the 13 study species. Species are ordered by sensitivity to encroachment (as in Fig. 1). *Gray bands* representing confidence intervals are shown for significant linear relationships. The scale of the *Y* axis varies among species to highlight changes in *S*/*R* across the light gradient rather than differences among species. See Online Resource 5 for regression statistics

to change for meadow species. For example, in forests in which light is assumed to be the limiting resource in the understory, root-trenching studies demonstrate the importance of competition with tree roots in limiting herbaceous production (Riegel et al. 1992, 1995; Lindh et al. 2003). Thus, an index of sensitivity to encroachment based on light availability alone may fail to account for important changes in soil resources or biotic factors (e.g., microbial or mycorrhizal communities) that mediate nutrient availability or acquisition by plants.

Interestingly, changes in biomass allocation with shading differed for the two species that appeared least sensitive to conifer encroachment. Allocation to shoots decreased in *A. millefolium* but increased in *I. chrysophylla*. In *A. millefolium*, declines were non-significant for shoot and root mass, but were significant for their ratio. In contrast, in *I. chrysophylla*, both shoot and root mass declined significantly, but more rapidly for roots—almost seven times that of shoots. These patterns suggest contrasting strategies of persistence given the morphological constraints of these

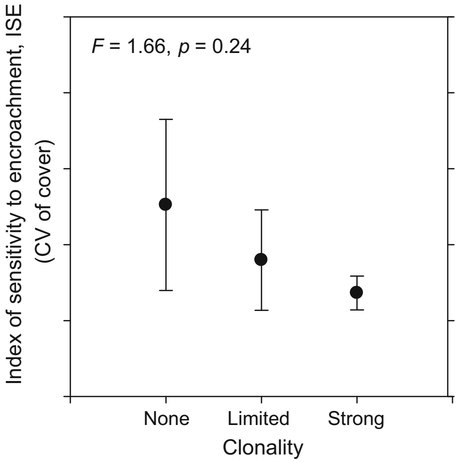

Fig. 6 Mean (±1 SD) sensitivity to encroachment (ISE) of species representing each of the three clonal groups: none (non-clonal, $n = 5$ species); limited (limited lateral spread via tillers, short rhizomes, or branching caudices; $n = 6$ species); and strong (potential for extensive lateral spread via long rhizomes or stolons; $n = 2$ species). *F* and *p* values are from one-way ANOVA

species. In open meadows, *I. chrysophylla* develops a dense system of stout rhizomes giving rise to the smallest *S*/*R* of the species studied. These rhizomes provide a substantial carbohydrate reserve, which is gradually depleted over time in the shade (Zobel and Antos 1987). In contrast, *A. millefolium* develops a system of long and slender rhizomes, advantageous to foraging and ramet production, but not to storage. The decline of *S*/*R* in the shade probably occurs because reproductive stems are a large part of shoot mass and these are rarely produced in the shade (Zeevaart 1962, J. Celis, unpublished data). Thus, for *A. millefolium,* the apparent shift in allocation to root systems may be a developmental constraint, not a response to changing resource conditions.

Sensitivity to encroachment did not relate to intraspecific variation in shoot height. Some species produced longer (etiolated) shoots in the shade, as expected (de Kroon and Hutchings 1995; Schmitt et al. 1995), but others produced shorter shoots, suggesting insufficient carbon gain to support height growth (Mulligan et al. 1997). However, the direction and magnitude of change among species did not correlate with ISE. For some species, reduced shoot growth may relate to the absence of reproduction under low levels of light (Lettow et al. 2014). In most of our study species (*I. chrysophylla* and *Viola nuttallii* are exceptions), shoot growth is intimately linked to flower production, which is greatly reduced under the canopy (J. Celis, unpublished data).

Finally, sensitivity to encroachment did not appear related to clonality. Although there was a trend toward reduced sensitivity among species with greater clonal potential, the small number of species or large variation within groups limited our ability to demonstrate a significant relationship. It is possible that the ability to forage laterally via rhizomes or stolons may provide little advantage if the spatial scales at which resources vary are greater than the distances plants can spread. Alternatively, non- or weakly clonal species may survive shading by other mechanisms, including changes in leaf morphology, physiology, or other traits (Pearcy and Sims 1994; Gianoli and Saldaña 2013). For example, many forest understory species are not clonal but survive under low light by reducing investment in sexual reproduction (Honnay et al. 2005).

Conclusions

We demonstrate that meadow species, which are typically adapted to high light conditions, can exhibit considerable variation for some morphological traits related to light capture. However, this intraspecific variation, which ultimately reflects phenotypic plasticity, ecotypic variation, or both, offers limited insight into the differences in species' persistence during conifer encroachment. The trend in leaf area was the only result consistent with expectation: sensitivity to encroachment was lower for species that produced larger leaves in the shade, presumably enhancing light interception. Conversely, few species shifted allocation from below- to above-ground structures as light levels declined. This suggests that changes in soil resources or biotic factors that affect nutrient availability or uptake may be as important as light. Or, it may indicate that the ability of plants to shift allocation of biomass is constrained by morphological or developmental characteristics that are fixed or linked to other traits (e.g., reproduction). The lack of strong relationships between persistence and morphological variability under declining levels of light points to the need for further study of species' physiological traits and of relationships with other potentially limiting factors during the transition from meadow to forest.

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Compliance with ethical standard

Conflict of interest The authors declare that they have no conflict of interest.

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