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Consequences of reduced light for flower production in conifer-invaded meadows of the Pacific Northwest, U.S.A

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Abstract Woody-plant encroachment threatens the biodiversity and ecosystem functioning of grasslands and meadows worldwide. An important but rarely described consequence of the transition to woody-plant dominance is the reduction in flowering of herbaceous species. We modeled community-wide relationships between flowering and light in two tree-invaded meadows (BG and M1) in the western Cascade Range, Oregon (USA). At BG, trees established over two centuries, forming a gradient of encroachment states (open meadow to old forest) and declining levels of light (91% to 8%), with most (85%) of the decline occurring within 2–4 decades of tree establishment. At M1, where trees formed distinct edges, we also tested whether distance from edge can serve as proxy for light in modeling flowering response. Flowering declined significantly with reductions in light at both sites: for a 10-percentage-point reduction in light, probability of flowering decreased by 35% (BG) and 21% (M1), median flowering density (flowers per m^2) by 15% and 8%, and median flowering effort (density per unit cover) by 10% and 9%, respectively. At M1, distance to edge was a poorer predictor of flowering due to its nonlinear relationship with light: $> 80\%$ of the reduction in light occurred within 4.5 m of the edge. Our results reveal strong, nonlinear relationships of flowering in time (most rapid early in the invasion process) and space (steepest at the forest edge). In a landscape dominated by forests, conifer invasion of mountain meadows can reduce the local and larger-scale diversity of plants and their insect pollinators.

Keywords Conifer encroachment · Flower production · Meadow species · Light · Pollinators

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Introduction

Woody-plant encroachment into grasslands is occurring on a global scale (Archer et al. 1995; Scholes and Archer 1997; Briggs et al. 2005; Ratajczak et al. 2012; Niemandt and Greve 2016). Conversion of grasslands

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to shrublands, woodlands, or forests can have profound consequences for carbon, water, and nutrient cycling (Barger et al. 2011; Eldridge et al. 2011; O'Donnell and Caylor 2012); plant diversity (Haugo and Halpern 2007; Ratajczak et al. 2012); and for trophic interactions (e.g., plant–pollinator networks) (Mustajärvi et al. 2001; Aizen et al. 2002; Aguilar et al. 2006; Ceballos et al. 2010; Hadley and Betts 2011).

In the largely forested western Cascade Mountains of Oregon, montane grasslands and meadows occupy a small fraction of the landscape, but are centers of biodiversity, supporting 85% of the western Cascades flora (Hickman 1976). Since the mid-1900s, encroachment by conifers has reduced the area of meadow in some portions of the western Cascades by more than 50% (Dailey 2007; Takaoka and Swanson 2008). Recent encroachment has been attributed to extrinsic factors—changes in climate, fire, or grazing regime that alter the competitive balance between herbaceous species and trees (Vale 1981; Miller and Halpern 1998; Hadley 1999; Takaoka and Swanson 2008)—and to strong internal feedbacks (tree–tree interactions) that accelerate the invasion process once trees establish (Miller and Halpern 1998; Halpern et al. 2010; Rice et al. 2012).

Tree invasion into meadows can reduce habitat quality for light-dependent flowering plants and the insect pollinators that depend on them (Highland et al. 2013; Dorado and Vazquez 2014; Jones et al. 2019). Reduced pollinator activity may, in turn, affect the reproduction, gene flow, and genetic diversity of meadow species (Campbell and Halama 1993; Mustajärvi et al. 2001). Whether habitat-related declines in plant populations precede, or follow, declines in insect pollinators is unclear, although a recent review of the literature suggests that for obligate-outcrossing plants and specialist pollinators, the two are inextricably linked, declining in tandem (Biesmeijer et al. 2006).

Light is likely to be the primary resource limiting flowering of grassland or meadow species. Studies of diverse taxonomic and functional groups demonstrate strong correlations between flowering and light (Jensen and Meyer 2001; Lugassi-Ben-Hamo et al. 2010; Zhao et al. 2012; Paradiso and Pascale 2014). In insular grasslands, Albrecht et al. (2016) found that flowering and fruit set in *Astragalus bibullatus*, a rare ecotonal species, were more sensitive to changes in tree cover than to changes in edaphic or understory conditions. Even in naturally shaded environments, light can be critical to flowering. For example, low-intensity thinning of a young coniferous forest in western Oregon enhanced rates of flowering among a diversity of forest herbs without increasing plant cover (Lindh 2008). Species of more open habitats, such as grasslands or meadows, should be particularly sensitive to reductions in light, although there are surprisingly few studies of flowering responses to tree encroachment (e.g., Albrecht et al. 2016).

In this study, we characterize community-wide relationships between flowering and light in two western Cascade meadows with distinctly different histories and spatial distributions of tree encroachment. The first site, Bunchgrass Ridge (BG), has been the subject of intensive studies of the encroachment process, including the timing and spatial patterning of tree invasion (Halpern et al. 2010; Rice et al. 2012) and its consequences for vegetation and soils (Griffiths et al. 2005; Haugo and Halpern 2007, 2010; Lang and Halpern 2007). Two centuries of invasion have created a diffuse mosaic of encroachment states (including remnant meadow openings to $>$ 140-year-old forests) and light environments (Haugo and Halpern 2007). The second site, M1, was invaded more recently (Jones 2016); trees form discrete edges with meadows to produce steep gradients in light. In combination, the two sites provide a unique opportunity to explore how the time course of invasion (BG) and distance to forest edge (M1) influence the availability of light and the production of flowers by meadow species. We consider three aspects of flowering: probability, density (flowers per m^2), and effort (density per unit cover, a measure of allocation to reproduction). We address the following questions:

Q1 How are flowering probability, density, and effort affected by reductions in light?
Q2 Do these relationships vary among species? If so, do species that show steeper declines in cover across the light gradient also show steeper declines in flowering effort (allocation to reproduction)?
Q3 Can distance from forest edge be used as a proxy for light in predicting flowering probability, density, or effort?

Methods

Study sites

We conducted this study in two mountain meadows occupying distinctly different landforms with differing histories and spatial distributions of tree encroachment. The first, Bunchgrass Ridge (BG), forms a gently sloping plateau at ~ 1350 m elevation (44°17′N, 121°57′W) along the western edge of the High Cascades Province in Oregon (Online Resource 1). Soil profiles at BG indicate that grassland has dominated the vegetation for centuries, if not millennia, and only recently have trees invaded (D. Lammers, personal communication). Soils are deep (> 170 cm), fine to very fine sandy loams, derived from andesitic basalt and tephra with varying amounts of glacially derived rock. They grade from Vitric Melanocryands in open meadows to Aquic Vitricryands in areas of older invading forests. The primary tree species, *Pinus contorta* and *Abies grandis*, established during two broad periods beginning in the nineteenth century (Haugo and Halpern 2007; Rice et al. 2012). The first wave of invasion (early- to late-1800s) was sparse but left most areas of meadow close to seed sources, facilitating the more rapid and denser invasion in the mid- to late-1900s. Two centuries of tree establishment and growth have created a diffuse mosaic of encroachment states encompassing remnant meadow openings, young forests (< 40 years), and older forests (> 140 years). Across this chronosequence, most (85%) of the reduction in light occurs early in the invasion process—within two to four decades of tree establishment— while tree densities are still low (< 200 stems/ha; Fig. 1; Haugo and Halpern 2007). Open meadows support mesic- and dry-site forbs and graminoids characteristic of the western Cascades (McCain et al. 2014). However, as trees establish, these species are replaced by shade-tolerant forest herbs (Haugo and Halpern 2007, 2010; Celis et al. 2017).

The second site, M1, is a small meadow opening within a larger complex of forests and meadows along Frissell Ridge, at the eastern boundary of the H. J. Andrews Experimental Forest, Oregon (44°14′47″N, 122°07′38″W) (Online Resource 2). M1 occurs on a steep (35–50%) southwest-facing slope below a ridgeline at 1445–1540-m elevation—a common position for upland meadows in the western

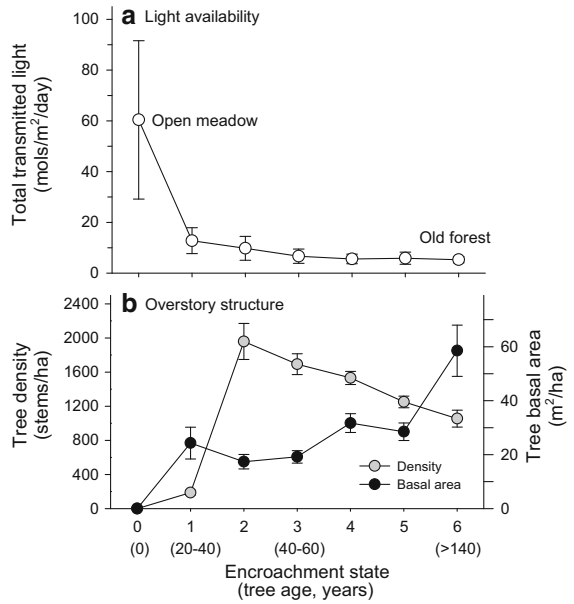

Fig. 1 Changes in **a** total transmitted light and **b** forest structure across a chronosequence of tree-invaded meadows at BG (modified from Haugo and Halpern 2007). Values are means (± 1 SD) of 17–84 subplots (10 × 10 m) per encroachment state. Encroachment states were based on a classification of the tree age structure in a subplot; classification variables were densities of trees (≥ 1.4 m tall) in each of 11, 20-year age bins. Primary ages are noted on the X axis. Encroachment state 0 represents residual meadow openings (no trees). States 1–5 represent the transition from open meadow to young forest (*Pinus contorta* and *Abies grandis* establishing between ~ 1920 and 1980), with age increasing and *Abies* becoming more dominant. State 6 represents 'old forest' (initial establishment ~ 1820) with *Abies* dominating the overstory and subcanopy

Cascade Range (McCain et al. 2014). In contrast to BG, soils at M1 are shallow (but well drained), formed in residuum or colluvium (Holderman-Rockdirt complex; NRCS 2018). The earliest invasion by *Abies amabilis, A. grandis*, and *Pseudotsuga menziesii* occurred in ~ 1870, but was very sparse. Invasion accelerated rapidly after 1940 (Jones 2016), progressing from both west- and east-facing edges toward the center of the meadow (Online Resource 2). Tree heights at the edge range from ~ 10–20 m. The meadow flora is richer than at BG, reflecting the greater diversity of microhabitats, although many species are common to both sites.

The climate of this region is maritime, characterized by cool, wet winters and warm, dry summers. Data from Santiam Pass, the nearest weather station at

comparable elevation (1488 m) are illustrative. Average minimum and maximum temperatures are − 6.6 °C and − 0.2 °C in December and 6.5 °C and 22.1 °C in August. Annual precipitation averages ~ 2290 mm, but is highly seasonal, with 14% falling from June through September (data from 1981 to 2010; Western Regional Climate Center; https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?or7559). Annual snowfall can exceed 11 m and snow can persist into May or early June (data from 1948 to 1985; Western Regional Climate Center; https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?orsant).

Sampling designs

We used different methods to sample the contrasting patterns of encroachment and light at BG and M1. At BG, characterized by a diffuse mosaic of remnant meadow openings and variously aged forests, we sampled in and adjacent to three 1-ha plots used as controls for a meadow restoration (tree removal) experiment (Online Resource 1; Halpern et al. 2012, 2016, 2019). Each of these plots was gridded into 100 subplots (10 × 10 m), a scale at which there was considerable variation in forest age, structure, and light (Haugo and Halpern 2007). Additional temporary plots were established adjacent to the 1-ha experimental plots to increase the sample of open meadow (Online Resource 1); these were also gridded into 10 × 10 m subplots. From the full set of subplots, we selected 80, distributed across four broadly defined encroachment states to ensure full representation of the light gradient: open meadow distant from forest edge; small residual meadows surrounded by forest; young, open forests; and old, closed-canopy forests (Celis et al. 2017). In each subplot, we measured light and flower production in four, 1 × 1 m quadrats spaced 1 m apart along a diagonal transect (Online Resource 1).

At M1, where forest–meadow boundaries were sharper, we established 11, 26-m-long transects perpendicular to the forest edge (Online Resource 2). Distinct edges were chosen to ensure rigorous tests of our third question: can distance from edge be used as a proxy for light in predicting flower production? With one exception, transects were separated by at least 15 m at increasing elevation on the slope (Online Resource 2). Approximately equal numbers were located on east- and west-facing edges. Each transect originated 7 m inside the canopy drip line and extended an additional 19 m into meadow (Online Resource 2). Measurements were made in contiguous quadrats (1 × 1 m) for 3 m on both sides of the edge, then in quadrats spaced 1 m apart beyond these. In total, each transect had five quadrats in the forest and 11 in the meadow. For analytic purposes, distance from edge was defined by the quadrat midpoint (e.g., − 0.5 m [forest], 0.5 m [meadow], 1.5 m, etc.).

We sampled at three times during the 2014 growing season at BG (May 24–June 8, June 29–July 1, and July 25–August 1) and twice at M1 (June 26 and July 21–22). On each date, we recorded the number of flowers per species in each quadrat. For species with 'simple' inflorescences (single flowers, racemes, or panicles), we counted all flowers. For species with small flowers in complex branching or 'compound' inflorescences (e.g., taxa in the Asteraceae), we counted inflorescences (Online Resources 3 and 4 list species' inflorescence types). At the last sampling date (typically peak abundance), we visually estimated the vertical projection of cover of each species as a percentage of the quadrat. Plant nomenclature follows the USDA Plants Database (USDA and NRCS 2019).

We took a hemispherical photograph of the canopy to quantify the light environment above each quadrat. Although direct measurements of light are ideal, they are difficult to achieve. Analysis of canopy images derived from hemispherical photographs provides an efficient and repeatable method for comparing multiple locations spanning a wide range of light levels (Welles and Cohen 1996; Machado and Reich 1999; Engelbrecht and Herz 2001; Bellow and Nair 2003; Seidel et al. 2011). Photos were taken between July 28 and August 29, 2014 using a Nikon Coolpix 990 digital camera with FC-E8 fisheye converter leveled on a tripod at a height of 0.7 m. Photos were taken at dawn or dusk, or during overcast conditions to avoid reflected light. Images were analyzed with the software Gap Light Analyzer 2.0 (GLA; Frazer et al. 1999), employing the standard overcast sky model. We express light availability as total transmitted light (% of available light) over the growing season (April through September).

Analysis

Prior to analysis, we dropped species from a site if they were present in fewer than 10% of quadrats; this

ensured a sufficient number of data points per species. We also dropped three species at M1 that were common but never flowered. From among the two or three sampling dates, we selected the maximum flower count for each species in each quadrat to represent peak flowering. Because the date of peak flowering varied among and, to a lesser extent, within species (Online Resource 5), our analyses represent a temporally integrated picture of the relationship between flowering and light.

To account for variation in flowering density due to variation in plant cover, we computed 'flowering effort' as the flowering density per unit cover. Flowering effort can be viewed as a measure of reproductive allocation, independent of cover.

Relationships of flowering to light (Q1)

We analyzed the relationships of flowering to light separately for each site. Due to the frequency of nonflowering events, we used a two-stage 'hurdle-model' approach (Zuur et al. 2009). In the first stage, we used the presence or the absence of flowers of each species in each quadrat as a binary response. In the second stage, we removed records of the presence with no flowers, then modeled flowering density or effort as a continuous response. Transect and quadrat were included as random intercepts to account for nesting of quadrats within transects. Light was treated as a fixed effect. It was not possible to include species or the species × light interaction as fixed effects: data were too sparse for some species and unevenly distributed across the light gradient for others. Moreover, pairwise comparisons of slopes (rates of decline in flowering) would be impractical due to the large number of species. Instead, we modeled community-wide relationships, accounting for the variation among species as a correlated random intercept and slope (based on the expectation that intercepts and slopes covary; Barr et al. 2013). To quantify the average proportion of total variance explained by species, we used the procedures of Johnson (2014).

For the first stage of the modeling process—probability of flowering—we fit a binomial generalized linear mixed model (GLMM) with a logit link. For the second stage—flowering density and effort—we used linear mixed models (LMMs) on log-transformed response data. Due to the logit link and log transformations, the estimated slopes of the relationships with light represent multiplicative changes. We express these as a percent reduction in odds of flowering (GLMMs) or in median flowering density or effort (LMMs), for a 10-percentage-point reduction in light—an ecologically meaningful change given the range of light. Annual species were excluded from the GLMMs because they always flowered (as expected, given the life history), but were included in the LMMs, because flowering density and effort varied.

To assess the statistical significance of the fixed effect (light), we used likelihood ratio Chi-squared tests for the GLMMs and Satterthwaite-adjusted *F*-tests for the LMMs. At M1, where we sampled east- and west-facing edges, we initially tested whether relationships to light varied with exposure. We found no statistical evidence of an interaction, and thus we present results of the simpler model with light as the only fixed effect.

Variation among species in the relationship to light (Q2)

As we were unable to assess variation in species' responses to light as a fixed effect (see "Relationships of flowering to light [Q1]"), we assessed the variation qualitatively, using a series of scatterplots to explore trends in flowering density and effort among species. We then used flowering effort data from BG to test whether species that show steeper declines in cover also show steeper declines in flower production across the light gradient (second part of Q2). For each of 15 species (present in > 10% of quadrats spanning the range of light levels), we computed two indices of sensitivity to light: ISE, sensitivity of cover, and IFE, sensitivity of flowering effort. ISE is described in full in Celis (2015) and Celis et al. (2017), a companion study of variation in plant functional traits. Briefly, for each species, we regressed nonzero values of cover (%) on total transmitted light (%) to fit a local polynomial regression model using the loess function (R Core Team 2018). From predicted values of cover at 0.1% increments of light, we computed a coefficient of variation (CV) for each species. Lower CV equates to lower variation or sensitivity of cover to light (little change over the light gradient); higher CV equates to greater sensitivity (consistent with a steeper slope). Simulations confirm that the CV can serve as a robust index of sensitivity to light when slope parameters or

model forms (exponential, linear, and quadratic) differ among species (Celis 2015).

IFE was computed similarly to quantify the relationship between flowering effort and light. However, to standardize among species with different rates of flower production, flowering effort was relativized for each species based on its maximum among quadrats (yielding a range of 0–1). Based on ISE and IFE values for each species (n = 15), we computed the Spearman's rank correlation, assessing statistical significance with the cor.test and spearmanCI functions (R Core Team 2018).

Distance from forest edge as a proxy for light (Q3)

Using data from M1, we tested whether distance from forest edge can serve as a proxy for light in predicting flowering presence, density, or effort. We used the light-based models described previously (GLMM with logit link, LMMs with log-transformed response), but substituted distance for light. We express estimated slopes as a percent change in odds of flowering, or in median flowering density or effort, for a 1-m shift toward the transect origin in the forest. As with the light-based models, we used likelihood ratio Chi-squared tests (GLMMs) or Satterthwaite-adjusted F-tests (LMMs) to assess the statistical significance of distance. We then compared the fits of the distance and light models based on the variation explained by the fixed effect (marginal R-squared; Nakagawa and Schielzeth 2013).

All analyses were conducted in R 3.2.1 (R Core Team 2018). Mixed models were fit using the lme4 package (ver. 1.1–12, Bates et al. 2014). For LMMs, F-tests with Satterthwaite degrees of freedom were performed using the lmerTest package (ver. 2.0–33, Zeileis and Hothorn 2002). Normality and homogeneity of variance (LMM) and model fit (GLMM) were assessed using residual plots generated from the DHARMa package (ver. 0.1.5, Hartig 2017).

Results

We recorded a greater number of species at M1 (52) than at BG (28), despite the lower intensity of sampling at M1. However, a greater proportion of species met the 10% frequency threshold for inclusion in the analyses at BG than at M1 (57 vs. 52%, Online Resources 3 and 4).

Relationships of flowering to light (Q1)

Probability of flowering showed a steep, nonlinear decline with reductions in light. For a 10-percentage-point reduction in light, estimated odds of flowering decreased at BG by 35.3% (CI 27.4–42.4%) and at M1 by 20.7% (CI 14.1–26.8%) (Table 1; Fig. 2a, b). Light accounted for considerably more of the variation at BG than at M1 (R^2_m of 23.5% vs. 5.5%; Table1); however, the variation attributable to species was comparable between sites (24.3% vs. 28.2%; Table 1).

Among quadrats in which species flowered, reductions in light also reduced flowering density and effort. For a 10-percentage-point reduction in light, estimated median flowering densities decreased at BG by 14.8% (CI 6.8–22.1%) and at M1 by 8.0% (CI 3.0–12.8%) (Table 1; Fig. 2c, d). Similarly, estimated median flowering effort decreased at BG by 10.2% (CI 3.9–16.1%) and at M1 by 8.7% (CI 4.8–12.6%) (Table 1; Fig. 2e, f). Despite the statistical significance of these relationships, light accounted for little of the variation in flowering density or effort at either site (range of R^2_m: 1.0–6.5%; Table 1). In contrast, species accounted for most variation: 35% (BG) and 36% (M1) for flowering density; 38% (BG) and 70% (M1) for flowering effort (Table 1).

Variation among species in the relationship to light (Q2)

Scatterplots of flowering performance suggest considerable variation in species' responses to light (Figs. 3 and 4; Online Resources 6 and 7). For example, at BG, *Eucephalus ledophyllus* was less likely to flower at low light than was *Fragaria virginiana* or *Hieracium scouleri* (compare distributions of open circles in Fig. 3). Similarly, for some species, flowering effort declined steeply from peak levels, with only a small reduction in light (*Eucephalus ledophyllus*, *Lupinus latifolius*, and *Symphyotrichum spathulatum* var. *spathulatum;* Fig. 3), but for others it declined more gradually (e.g., *Erigeron aliceae*; Figs. 3 and 4). Finally, for *Fragaria virginiana*, peak flowering effort did not occur at maximum light (Fig. 3). This wide variation in sensitivity to light was reflected in the

Table 1 Results of generalized and linear mixed models (GLMMs and LMMs) relating flowering probability, density (number per m^2), and effort (density per unit cover) to reductions in total transmitted light (BG and M1) or to distance from transect origin in the forest (M1 only)

Response (model type)	Fixed effect	Site	Est. slope (%)	95% CI	χ^2	F	df	P	$R^{2\,a}_m$	R^{2b}_c	Random effects[c]		
											Species	Transect	Quadrat
Flowering probability (GLMM)	Light	BG	− 35.3	− 27.4, − 42.4	25.2	–	1	< 0.001	0.235	0.530	0.243	0.052	0.000
		M1	− 20.7	− 14.1, − 26.8	26.4	–	1	< 0.001	0.055	0.342	0.282	0.005	0.000
	Distance	M1	− 7.1	− 4.1, − 10.0	13.7	–	1	0.002	0.046	0.344	0.292	0.006	0.000
Flowering density (LMM)	Light	BG	− 14.8	− 6.8, − 22.1	–	12.3	1, 18.9	0.002	0.065	0.596	0.350	0.037	0.000
		M1	− 8.0	− 3.0, − 12.8	–	9.5	1, 19.0	0.006	0.011	0.386	0.359	0.014	0.004
	Distance	M1	− 0.6	1.0, − 2.2	–	0.5	1, 24.1	0.486	0.001	0.386	0.368	0.016	0.014
Flowering effort (LMM)	Light	BG	− 10.2	− 3.9, − 16.1	–	9.6	1, 16.0	0.007	0.052	0.461	0.381	0.027	< 0.001
		M1	− 8.7	− 4.8, − 12.6	–	17.7	1, 15.0	< 0.001	0.010	0.716	0.696	0.010	0.000
	Distance	M1	− 1.5	− 0.3, − 2.8	–	6.0	1, 14.1	0.027	0.004	0.712	0.700	0.009	0.000

Estimated slopes represent multiplicative changes (in percent) in odds of flowering or in median flowering density or effort, for a 10-percentage-point reduction in light or a 1-m shift toward the transect origin. Flowering density and effort were log transformed. P values are for tests of the fixed effect (light or distance), based on likelihood ratio χ^2 tests (GLMM) and Satterthwaite adjusted F tests (LMM). For graphed relationships, see Fig. 2

[a] R^2_m (marginal) is the variation explained by the fixed effect

[b] R^2_c (conditional) is the variation explained by both fixed and random effects

[c] Proportion of total variation explained by the random effects (species and sampling units), including all aspects of variation around the estimated relationship (intercept and slope). Values are the average proportion of variation explained, i.e., averaging the variance across each value of light (Johnson 2014)

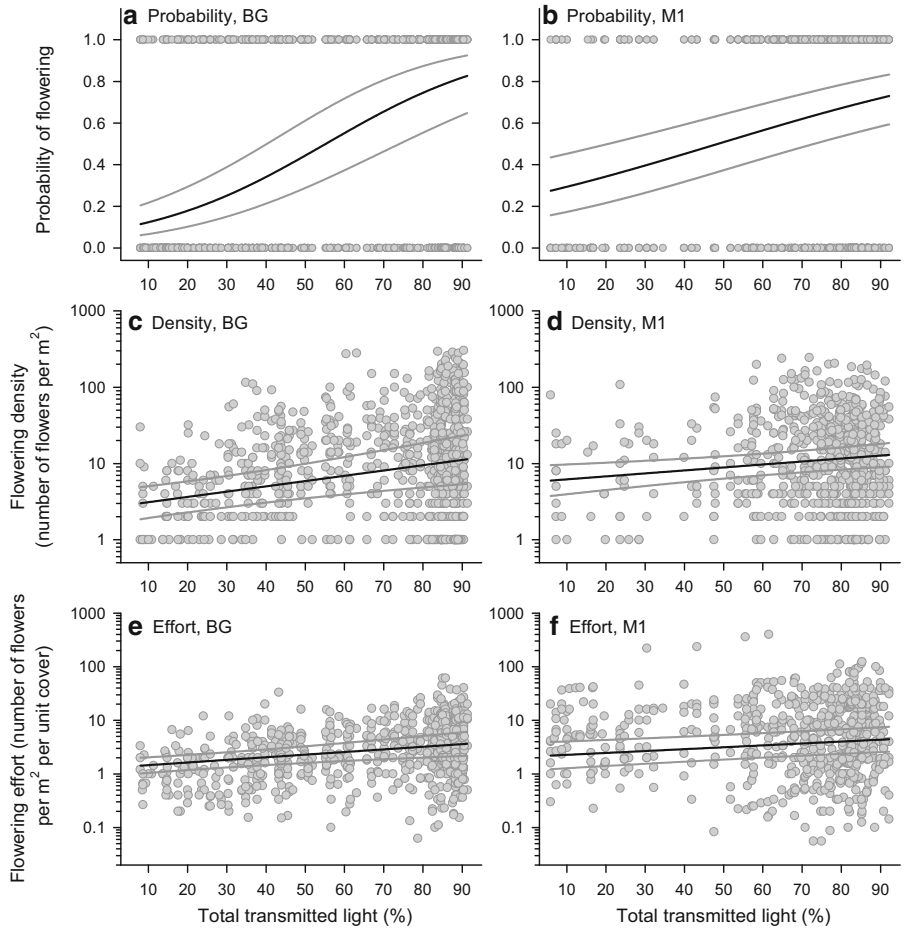

Fig. 2 Predicted values and 95% CIs from binomial generalized linear mixed models (GLMMs) and linear mixed models (LMMs) of the relationships between flowering and total transmitted light (%) at BG (left) and M1 (right). **a**, **b** Probability of flowering, **c**, **d** flowering density (number of flowers or inflorescences per m^2), and **e**, **f** flowering effort (density per unit cover). Density and effort models exclude values of zero. Note the log scale of the response. Data points represent quadrat-scale values of individual species

broad range of IFE values at BG (Fig. 5). Although species also showed wide variation in sensitivity of cover (ISE), the indices varied independently, yielding a weak correlation that was not statistically significant (*rho* = − 0.28, CI − 0.96–0.42; $P = 0.31$; Fig. 5).

Distance from forest edge as a proxy for light (Q3)

At M1, where we tested whether distance from edge could serve as a proxy for light, mean levels of light declined steeply across the edge (Fig. 6). Over a distance of 3 m (+ 1.5 to − 1.5 m) light levels declined > 75%. Across quadrats in the meadow (0.5–18.5 m), 60% of the decline in light occurred within 4.5 m of the edge.

Relationships with distance were either statistically significant, but weaker, than the corresponding relationship with light (flowering probability and effort), or they were not statistically significant (flowering density) (Table 1). With a 1-m shift toward the forest, estimated odds of flowering declined by 7.1% (CI 4.1–10.0%), estimated median density by 0.6% (− 1.0–2.2%), and estimated median flowering effort by 1.5% (CI 0.3–2.8%). Distance explained less variation than did light (4.6% vs. 5.5% for probability; 0.1% vs. 1.1% for density; and 0.4% vs. 1.0% for effort; Table 1). Species accounted for most of the variation in distance-based models (29.2–70.0%; Table 1).

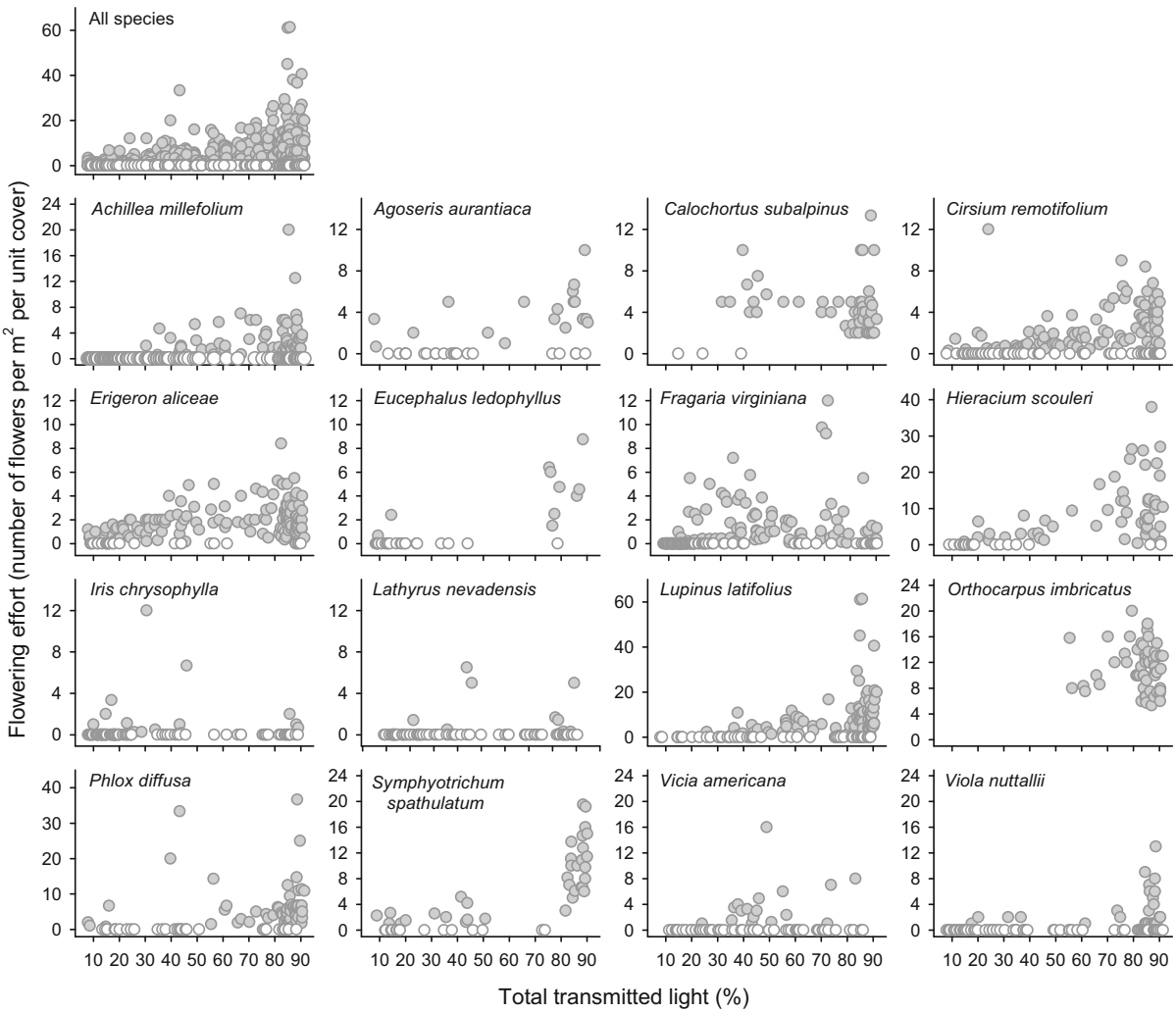

Fig. 3 Flowering effort (number of flowers or inflorescences per m^2 per unit cover) versus total transmitted light (%) for common species at BG (present in $\geq$ 10% of quadrats). See Online Resource 6 for plots of flowering density

Discussion

We examine an important, but rarely described consequence of the shift from herbaceous to woody-plant dominance of meadows—the community-wide decline in flower production. In two montane meadows of the western Cascade Range, we document strong effects of invading trees on flowering density and effort, reflecting light-related declines in the cover of meadow species and in their allocation to reproduction. Moreover, our results highlight the nonlinear nature of these relationships in time and space, with most of the reduction in light—thus the steepest decline in flowering—occurring early in the invasion process (at BG) or close to the forest edge (at M1).

Relationships of flowering to changes in light through time and space

Shading by invading trees resulted in substantial declines in flowering at both sites. Over the wide range of light levels at BG (91% to 8%), probability of flowering declined by an estimated 86%, and median density and effort by 74% and 61%. Over a comparable light gradient at M1 (from 92 to 1%), flowering probability, density, and effort declined by an estimated 65%, 56%, and 52%. Yet, more striking than

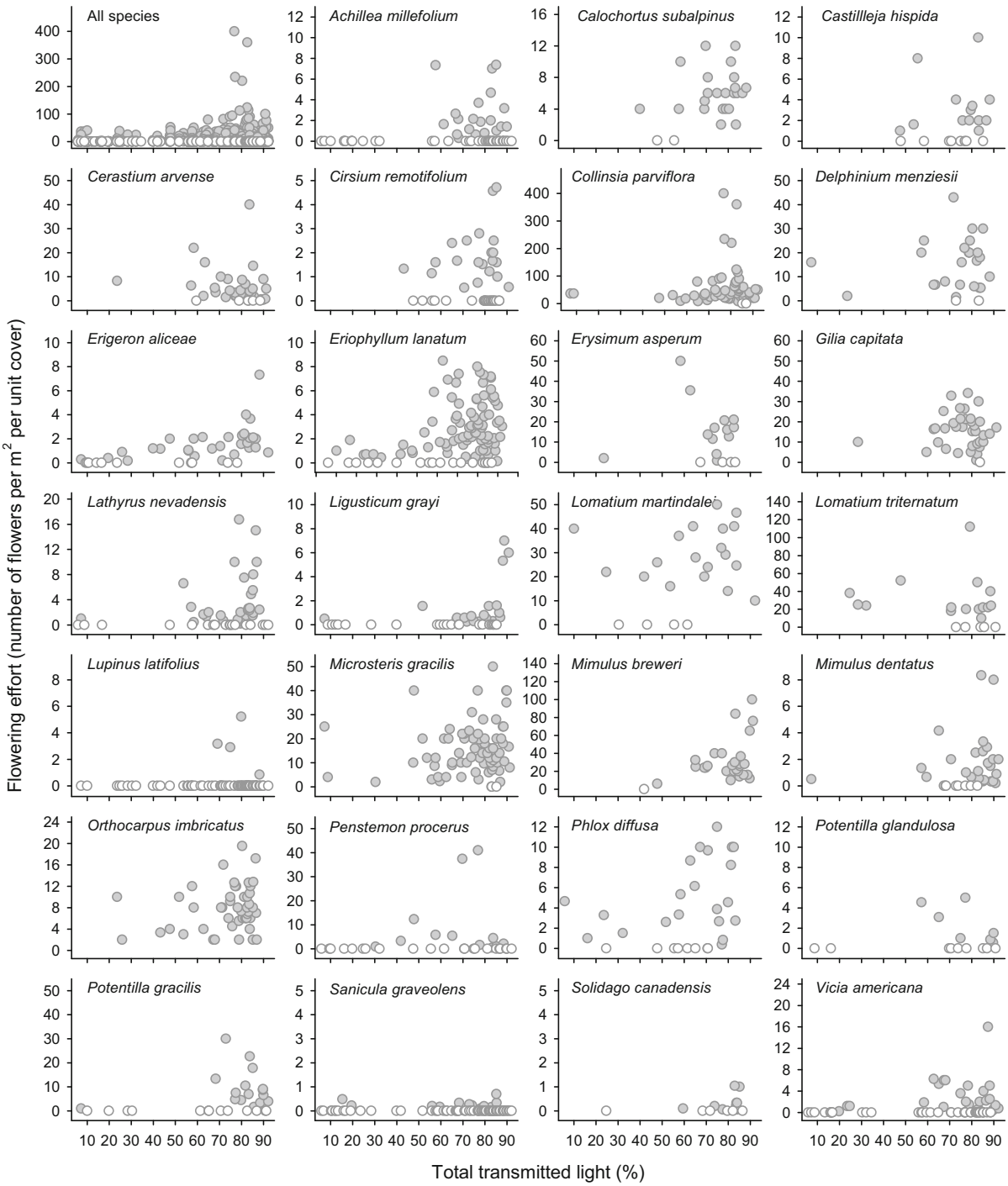

Fig. 4 Flowering effort versus total transmitted light (%) for common species at M1 (present in ≥ 10% of quadrats). See Online Resource 7 for plots of flowering density

these overall declines are the nonlinear rates at which they occur in time and space. For example, at BG, trees have invaded meadows for more than 140 years, yet 85% of the total reduction in light, thus most of the decline in flowering, occurs within the first two to four decades of tree establishment, when tree densities are

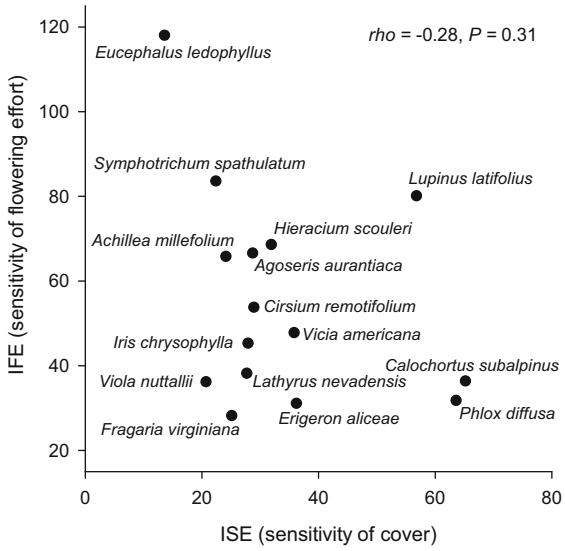

Fig. 5 Relationship between sensitivity of flowering (IFE) and sensitivity of cover to light (ISE) among common species at BG (present in ≥ 10% of quadrats across the light gradient). IFE and ISE are CVs of predicted values of flowering effort and cover, respectively. Higher values indicate more rapid declines in flowering (IFE) or cover (ISE) with reductions in light

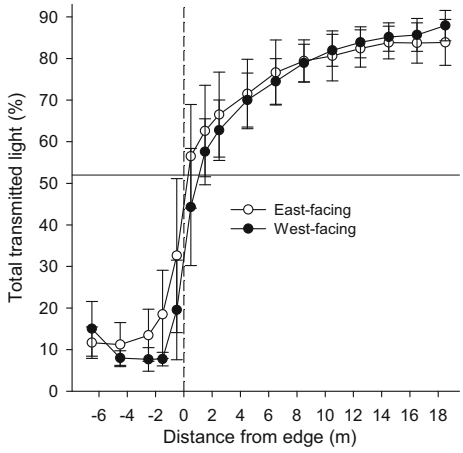

Fig. 6 Observed values of total transmitted light versus distance from forest edge for east- and west-facing transects at M1. Values are means ± 1 SD (n = 5–6)

still low (Fig. 1; Haugo and Halpern 2007). Similarly, at M1, more than 80% of the reduction in light, thus most of the decline in flowering, occurs within 4.5 m of the edge. The implications for meadow species are clear. When encroachment is diffuse (as it was at BG), most of the reduction in light occurs early in the invasion process while tree density remains low. Thus, flowering is suppressed well before species are extirpated. On the other hand, when encroachment forms an advancing edge (as at M1), the effects of shading, albeit strong, are spatially limited. Studies of edge-related gradients in forest and agricultural systems suggest that the strength and depth of forest influence—including effects on understory light—can vary with the structure of the edge (e.g., height and density of trees) or the physical environment (e.g., topography and edge exposure) (Cadenasso et al. 1997; Heithecker and Halpern 2007; Baker et al. 2013). At M1, trees were relatively short (10–20 m) but dense, resulting in a narrow zone of influence in the meadow and greatly reduced light in the forest.

Flowering effort as a measure of allocation to reproduction

We expected flowering density to decline with loss of species' cover (Haugo and Halpern 2007) and mass (Celis et al. 2017), consistent with the positive correlation in most plants between reproductive output and size (Aarssen and Taylor 1992; Aarssen and Jordan 2001; Weiner et al. 2009). Declines in flowering effort—which account for changes in cover—suggest, however, that some of the loss of flower production stems from reduced allocation to reproduction. Under conditions of limiting resources, plants face tradeoffs in allocation to reproduction, maintenance, and growth (Pitelka et al. 1980; Bazzaz and Reekie 1985). Theoretically, under declining levels of light, perennials (which dominated both meadow sites) should reduce allocation to flowers and root systems relative to leaves. Below a threshold size, reproduction may not even be possible (Weiner 2004), as suggested by the high frequency of nonflowering events at low light. For annuals, whose persistence depends on sexual reproduction, this size threshold is typically smaller (Weiner 2004). Thus, it is not surprising that annuals, which were common at M1, always flowered, albeit at reduced density. Others have observed community-wide increases in herbaceous flower production without detectable changes in cover when light *increases* after thinning or burning (Lindh 2008; Lettow et al. 2014). In our system, declining levels of light reduced both the cover and allocation of species to reproduction.

Variation in species' responses to light

Our community-wide census revealed substantial variation in species' relationships to light. For some species, flowering effort declined steeply with only small reductions in light. For others, it declined more slowly or peaked at intermediate levels of light. Nevertheless, we did not find a statistically significant correlation between sensitivity of flowering (IFE) and sensitivity of abundance (ISE) to light. Species that reduced allocation to reproduction more rapidly in the shade were not the same as those with steeper declines in cover. Several factors may contribute to this lack of correspondence: species may differ in their resource-allocation strategies when light is limiting; morphological constraints may limit plasticity in allocation (Celis et al. 2017); or resources other than light may affect patterns of allocation. In this study, we assumed that light was the limiting resource. Additional research is needed on the roles of other factors that can change with encroachment (e.g., soil moisture, nitrogen availability, microbial activity, or pH; Amiotti et al. 2000; Lindh et al. 2003; Griffiths et al. 2005; Bagaria et al. 2017).

Distance from forest edge as a proxy for light

At M1, discrete forest–meadow boundaries allowed us to test whether proximity to edge can serve as a proxy for light in predicting flowering responses to encroachment. We found that distance was a poorer predictor of flowering than was light. This result is not surprising given the sigmoidal relationship of light to distance: light remained low in the forest, rose steeply across the edge, then increased more slowly in the meadow. A model that predicts flower production indirectly from distance would need to capture this nonlinear relationship with light. However, it also would need to account for other factors that affect light transmission across the edge, e.g., tree height, edge density, and exposure.

Broader ecological and management implications

For meadow forbs and their insect pollinators, the consequences of tree invasion are inextricably linked (Aguilar et al. 2006; Burkle and Alarcón 2010; Sabatino et al. 2010). Flower, pollen, and nectar production require sufficient levels of light; pollinators respond both to light (Kilkenny and Galloway 2008) and to the diversity and abundance of floral resources (Kilkenny and Galloway 2008; Dauber et al. 2010; Cao et al. 2017); and plant reproductive success hinges on the activity of pollinators (Dauber et al. 2010; Cao et al. 2017). When changes in habitat quality or resource conditions alter one or more of these functional relationships, the diversity and abundance of both groups may decline together (Biesmeijer et al. 2006).

Recent studies in western Cascade meadows highlight the diversity and complexity of plant–pollinator networks (Helderop 2015; Jones 2019). Larger meadows support greater numbers of pollinators, although small isolated meadows with rocky or seasonally wet soils contribute to the broader diversity of plants and insects (Jones 2019). Although these interaction networks may be resilient to change because they are dominated by far-ranging generalists (Helderop 2015), they nevertheless remain susceptible to the cumulative effects of encroachment that degrade habitat quality. Our study offers unique insights into the time course and spatial extent of these effects. Provided that meadows remain sufficiently large (wider than several tree heights) effects of shading, albeit severe, are limited to a narrow band at the forest edge. In contrast, diffuse or dispersed invasion—even at low density—can lead to rapid reductions in light and flower production. Although many forbs can persist in the understory at low abundance or vigor for decades (Haugo and Halpern 2007; Celis et al. 2017), long-term reductions in flowering will have consequences for the genetic diversity of plants and the pollinators that depend on them. Mechanical removal of trees early in the invasion process will reduce the likelihood of species' extirpation, increase light and flower production, and maintain the diversity and complexity of plant–pollinator networks. On the other hand, subsequent burning to reduce woody fuels can have adverse effects on surviving species and promote expansion of a highly competitive sedge, inhibiting reassembly of the native community (Halpern et al. 2016, 2019).

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References

Aarssen LW, Jordan C (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. Ecoscience 8:471–477. https://doi.org/10.1080/11956860.2001.11682677

Aarssen LW, Taylor DR (1992) Fecundity allocation in herbaceous plants. Oikos 65:225–232. https://doi.org/10.2307/3545013

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Lett 9:968–980. https://doi.org/10.1111/j.1461-0248.2006.00927.x

Aizen MA, Ashworth L, Galetto L (2002) Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? J Veg Sci 13:885–892. https://doi.org/10.1111/j.1654-1103.2002.tb02118

Albrecht MA, Becknell RE, Long Q (2016) Habitat change in insular grasslands: woody plant encroachment alters the population dynamics of a rare ecotonal plant. Biol Conserv 196:93–102. https://doi.org/10.1016/j.biocon.2016.01.032

Amiotti NM, Zalba P, Sanchez LF, Peinemann N (2000) The impact of single trees on properties of loess-derived grassland soils in Argentina. Ecology 81:3283–3290. https://doi.org/10.1890/0012-9658(2000)081[3283:TIOSTO]2.0.CO;2

Archer S, Schimel DS, Holland EA (1995) Mechanisms of shrubland expansion: land use, climate or CO_2? Clim Change 29:91–99. https://doi.org/10.1007/BF01091640

Bagaria G, Roda F, Clotet M, Miguez S, Pino J (2017) Contrasting habitat and landscape effects on the fitness of a long-lived grassland plant under forest encroachment: do they provide evidence for extinction debt? J Ecol 106:278–288. https://doi.org/10.1111/1365-2745.12860

Baker SC, Spies TA, Wardlaw TJ, Balmer J, Franklin JF, Jordan GJ (2013) The harvested side of edges: effect of retained forests on the re-establishment of biodiversity in adjacent harvested areas. For Ecol Manage 302:107–121. https://doi.org/10.1016/j.foreco.2013.03.024

Barger NN, Archer SA, Campbell JL, Huang C, Morton JA, Knapp AK (2011) Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. J Geophys Res 116:G00K07. https://doi.org/10.1029/2010JG001506

Barr DJ, Levy R, Scheepers C, Tily HJ (2013) Random effects structure for confirmatory hypothesis testing: keep it maximal. J Mem Lang 68:255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using 'Eigen' and S4. R package version 1.1-7. https://CRAN.Rproject.org/package=lme4. Accessed 14 Feb 2018

Bazzaz FA, Reekie EG (1985) The meaning and measurement of reproductive effort in plants. In: White J (ed) Studies in plant demography: a Festschrift for John L. Harper. Academic Press, London

Bellow JG, Nair PKR (2003) Comparing common methods for assessing understory light availability in shaded-perennial agroforestry systems. Agric For Meteorol 114:197–211. https://doi.org/10.1016/S0168-1923(02)00173-9

Biesmeijer JC, Roberts SP, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354. https://doi.org/10.1126/science.1127863

Briggs JM, Knapp AK, Blair JM, Heisler JL, Hoch GA, Lett MA, McCarron JK (2005) An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. Bioscience 55:243–254. https://doi.org/10.1641/0006-3568(2005)055[0243:AEITCA]2.0.CO;2

Burkle LA, Alarcón R (2011) The future of plant–pollinator diversity: understanding interaction networks across time, space, and global change. Am J Bot 98:528–538. https://doi.org/10.3732/ajb.1000391

Cadenasso ML, Traynor MM, Pickett STA (1997) Functional location of forest edges: gradients of multiple physical factors. Can J For Res 27:774–782. https://doi.org/10.1139/x97-013

Campbell DR, Halama KJ (1993) Resource and pollen limitations to lifetime seed production in a natural plant population. Ecology 74:1043–1051. https://doi.org/10.2307/1940474

Cao GX, Wu BX, Xu XJ, Wang X, Yang CP (2017) The effects of local variation in light availability on pollinator visitation, pollen and resource limitation of female production in *Hosta ventricosa*. Bot Stud 58:24. https://doi.org/10.1186/s40529-017-0180-z

Ceballos G, Davidson A, List R, Pacheco J, Manzano-Fischer P, Santos-Barrera G, Cruzado J (2010) Rapid decline of a grassland ecosystem and its ecological and conservation implications. PLoS ONE 5:e8562. https://doi.org/10.1371/journal.pone.0008562

Celis J (2015) The role of intraspecific functional trait variation in the differential decline of meadow species following conifer encroachment. Thesis, Oregon State University, Corvallis

Celis J, Halpern CB, Jones FA (2017) Intraspecific trait variation and the differential decline of meadow species during conifer encroachment. Plant Ecol 218:565–578. https://doi.org/10.1007/s11258-017-0712-3

Dailey MM (2007) Meadow classification in the Willamette National Forest and conifer encroachment patterns in the Chucksney-Grasshopper Meadow Complex, western Cascade Range. Thesis, Oregon State University, Corvallis, Oregon

Dauber J, Biesmeijer JC, Gabriel D, Kunin WE, Lamborn E, Meyer B, Nielsen A, Potts SG, Roberts SPM, Sõber V, Settele J, Steffan-Dewenter I, Stout JC, Teder T, Tscheulin T, Vivarelli D, Petanidou T (2010) Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. J Ecol 98:188–196. https://doi.org/10.1111/j.1365-2745.2009.01590.x

Dorado J, Vázquez DP (2014) The diversity-stability relationship in floral production. Oikos 123:1137–1143. https://doi.org/10.1111/oik.00983

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–722. https://doi.org/10.1111/j.1461-0248.2011.01630.x

Engelbrecht BM, Herz HM (2001) Evaluation of different methods to estimate understorey light conditions in tropical forests. J Trop Ecol 17:207–224. https://doi.org/10.1139/X09-116

Frazer GW, Canham CD, Lertzman KP (1999) Gap light analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Users' manual and program documentation, Version 2.0. Simon Fraser University and the Institute of Ecosystem Studies, Burnaby and Millbrook

Griffiths R, Madritch M, Swanson A (2005) Conifer invasion of meadows transforms soil characteristics in the Pacific Northwest. For Ecol Manage 208:347–358. https://doi.org/10.1016/j.foreco.2005.01.015

Hadley AS, Betts MG (2011) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. Biol Rev 87:526–544. https://doi.org/10.1111/j.1469-185X.2011.00205.x

Hadley K (1999) Forest history and meadow invasion at the Rigdon Meadows archaeological site, western Cascades, Oregon. Phys Geogr 20:116–133. https://doi.org/10.1080/02723646.1999.10642672

Halpern CB, Antos JA, Kothari S, Olson AM (2019) Past tree influence and prescribed fire exert strong controls on reassembly of mountain grasslands after tree removal. Ecol Appl 29:e01860. https://doi.org/10.1002/eap.1860

Halpern CB, Antos JA, McKenzie D, Olson, M (2016) Past tree influence and prescribed fire mediate biotic interactions and community reassembly in a grassland-restoration experiment. J Appl Ecol 53:264–273. https://doi.org/10.1111/1365-2664.12570

Halpern CB, Antos JA, Rice JM, Haugo RM, Lang NL (2010) Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. J Veg Sci 21:717–732. https://doi.org/10.1111/j.1654-1103.2010.01183.x

Halpern CB, Haugo RD, Antos JA, Kaas SS, Kilanowski AL (2012) Grassland restoration with and without fire: evidence from a tree-removal experiment. Ecol Appl 22:425–441. https://doi.org/10.1890/11-1061.1

Hartig F (2017) Package DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1.5. https://CRAN.R-project.org/package=DHARMa. Accessed 10 Mar 2018

Haugo RD, Halpern CB (2007) Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. Botany 88:285–298. https://doi.org/10.1139/B07-024

Haugo RD, Halpern CB (2010) Tree age and tree species shape positive and negative interactions in a montane meadow. Botany 88:488–499. https://doi.org/10.1139/B10-018

Heithecker TD, Halpern CB (2007) Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. For Ecol Manage 248:163–173. https://doi.org/10.1016/j.foreco.2007.05.003

Helderop E (2015) Diversity, generalization, and specialization in plant-pollinator networks of montane meadows, western Cascades. Thesis, Oregon State University, Corvallis

Hickman JC (1976) Non-forest vegetation of the central western Cascade Mountains of Oregon. Northwest Sci 50:145–155

Highland SA, Miller JC, Jones JA (2013) Determinants of moth diversity and community in a temperate landscape: vegetation, topography, and seasonality. Ecosphere 4:129. https://doi.org/10.1890/ES12-00384.1

Jensen K, Meyer C (2001) Effects of light competition and litter on performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. Plant Ecol 155:169–181. https://doi.org/10.1023/A:1013270628964

Johnson PCD (2014) Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes models. Methods Ecol Evol 5:944–946. https://doi.org/10.1111/2041-210X.12225

Jones KE (2016) Spatio-temporal patterns of tree establishment in the M1 meadow of the HJ Andrews Experimental Forest. Thesis. Oregon State University, Corvallis

Jones JA, Hutchinson R, Moldenke A, Pfeiffer V, Helderop E, Thomas E, Griffin J, Reinholtz A (2019) Landscape patterns and diversity of meadow plants and flower-visitors in a mountain landscape. Landsc Ecol 34:997–1014. https://doi.org/10.1007/s10980-018-0740-y

Kato E, Hiura T (1999) Fruit set in *Styrax obassia* (Styracaceae): the effect of light availability, display size, and local floral density. Am J Bot 86:495–501. https://doi.org/10.2307/2656810

Kilkenny FF, Galloway LF (2008) Reproductive success in varying light environments: direct and indirect effects of light on plants and pollinators. Oecologia 155:247–255. https://doi.org/10.1007/s00442-007-0903-z

Lang NL, Halpern CB (2007) The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. Can J Bot 85:557–569. https://doi.org/10.1139/B07-051

Lettow MC, Brudvig LA, Bahlai CA, Landis DA (2014) Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. For Ecol Manage 329:89–98. https://doi.org/10.1016/j.foreco.2014.06.019

Lindh BC (2008) Flowering of understory herbs following thinning in the western Cascades, Oregon. For Ecol Manage 256:929–936. https://doi.org/10.1016/j.foreco.2008.05.055

Lindh BC, Gray AN, Spies TA (2003) Responses of herbs and shrubs to reduced root competition under canopies and in gaps: a trenching experiment in old-growth Douglas-fir forests. Can J For Res 33:2052–2057. https://doi.org/10.1139/x03-120

Lugassi-Ben-Hamo M, Kitron M, Bustan A, Zaccai M (2010) Effect of shade regime on flower development, yield and quality in lisianthus. Sci Hortic 124:248–253. https://doi.org/10.1016/j.scienta.2009.12.030

Machado J-L, Reich PB (1999) Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest

understory. Can J For Res 29:1438–1444. https://doi.org/10.1139/x99-102

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

Miller EA, Halpern CB (1998) Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. J Veg Sci 9:265–282. https://doi.org/10.2307/3237126

Mustajärvi K, Siikamäki P, Rytkönen S, Lammi A (2001) Consequences of plant population size and density for plant-pollinator interactions and plant performance. J Ecol 89:80–87. https://doi.org/10.1046/j.1365-2745.2001.00521.x

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Niemandt C, Greve M (2016) Fragmentation metric proxies provide insights into historical biodiversity loss of critically endangered grassland. Agric Ecosyst Environ 235:172–181. https://doi.org/10.1016/j.agee.2016.10.018

NRCS (National Resource Conservation Service) (2018) National cooperative soil characterization database. https://websoilsurvey.sc.egov.usda.gov/App/. Accessed 2 Dec 2018

O'Donnell FC, Caylor KK (2012) A model-based evaluation of woody plant encroachment effects on coupled carbon and water cycles. J Geophys Res 117:G02012. https://doi.org/10.1029/2011JG001899

Paradiso R, De Pascale S (2014) Effects of plant size, temperature, and light intensity on flowering of *Phalaenopsis* hybrids in Mediterranean greenhouses. Sci World J 2014:420807. https://doi.org/10.1155/2014/420807

Pitelka LF, Stanton DS, Peckenham MO (1980) Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). Am J Bot 67:942–948. https://doi.org/10.1002/j.1537-2197.1980.tb07724.x

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 21 Jan 2018

Ratajczak Z, Nippert JB, Collins SL (2012) Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703. https://doi.org/10.1890/11-1199.1

Rice JM, Halpern CB, Antos JA, Jones JA (2012) Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow. Plant Ecol 213:555–568. https://doi.org/10.1007/s11258-012-0021-9

Sabatino M, Maceira N, Aizen MA (2010) Direct effects of habitat area on interaction diversity in pollination webs. Ecol Appl 20:1491–1497. https://doi.org/10.1890/09-1626.1

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Ann Rev Ecol Syst 28:517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

Seidel D, Fleck S, Leuschner C, Hammett T (2011) Review of ground-based methods to measure the distribution of biomass in forest canopies. Ann For Sci 68:225–244. https://doi.org/10.1007/s13595-011-0040-z

Takaoka S, Swanson FJ (2008) Change in extent of meadows and shrub fields in the central western Cascade Range, Oregon. Prof Geogr 60:527–540. ISSN: 0033-0124

USDA, NRCS. 2019. The PLANTS database. National Plant Data Team, Greensboro, NC. https://plants.usda.gov. Accessed 6 Apr 2019

Vale TR (1981) Tree invasion of montane meadows in Oregon. Am Midl Nat 105:61–69. https://doi.org/10.2307/242501

Weiner J (2004) Allocation, plasticity and allometry in plants. Perspect Plant Ecol 6:207–215. https://doi.org/10.1078/1433-8319-00083

Weiner J, Campbell LG, Pino J, Echarte L (2009) The allometry of reproduction within plant populations. J Ecol 97:1220–1233. https://doi.org/10.1111/j.1365-2745.2009.01559.x

Welles JM, Cohen S (1996) Canopy structure measurement by gap fraction analysis using commercial instrumentation. J Exp Bot 47:1335–1342. https://doi.org/10.1093/jxb/47.9.1335

Xie XF, Hu YK, Pan X, Liu FH, Song YB, Dong M (2006) Biomass allocation of stoloniferous and rhizomatous plant in response to resource availability: a phylogenetic meta-analysis. Front Plant Sci 7:603. https://doi.org/10.3389/fpls.2016.00603

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10. https://CRAN.R-project.org/doc/Rnews/. Accessed 15 Mar 2018

Zhao D, Hao Z, Tao J (2012) Effects of shade on plant growth and flower quality in the herbaceous peony (*Paeonia lactiflora* Pall.). Plant Physiol Biochem 61:187–196. https://doi.org/10.1016/j.plaphy.2012.10.005

Zuur A, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

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Consequences of reduced light for flower production in conifer-invaded meadows of the Pacific Northwest, U.S.A.
Plant Ecology
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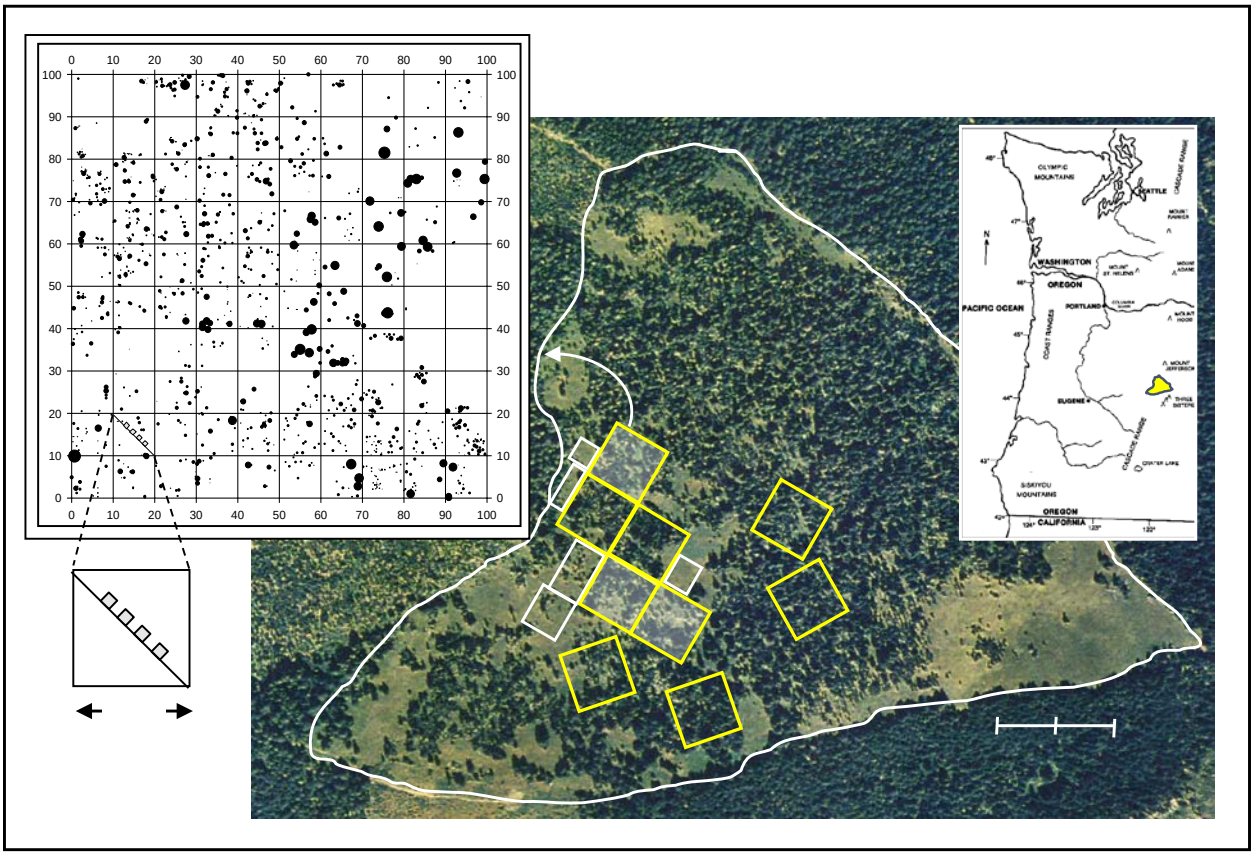
Online Resource 1. Location and aerial image of Bunchgrass Ridge (BG) on the western slope of the High Cascades, Oregon. The aerial photo shows the 1 ha (100 × 100 m) experimental plots, including three controls (yellow squares with white shading), and the smaller temporary plots in open meadows (white rectangles) used to measure flowering and light. A stem map from one of the experimental plots illustrates the mosaic of encroachment states (trees of varying age, density, and size); symbol size corresponds to tree diameter (from Haugo and Halpern 2007). We sampled 80, 10 × 10 m subplots in the three control and smaller temporary plots. In each subplot we estimated species' cover, counted flowers or inflorescences, and measured light (% total transmitted light from a hemispherical photograph) in four 1 m^2 quadrats.



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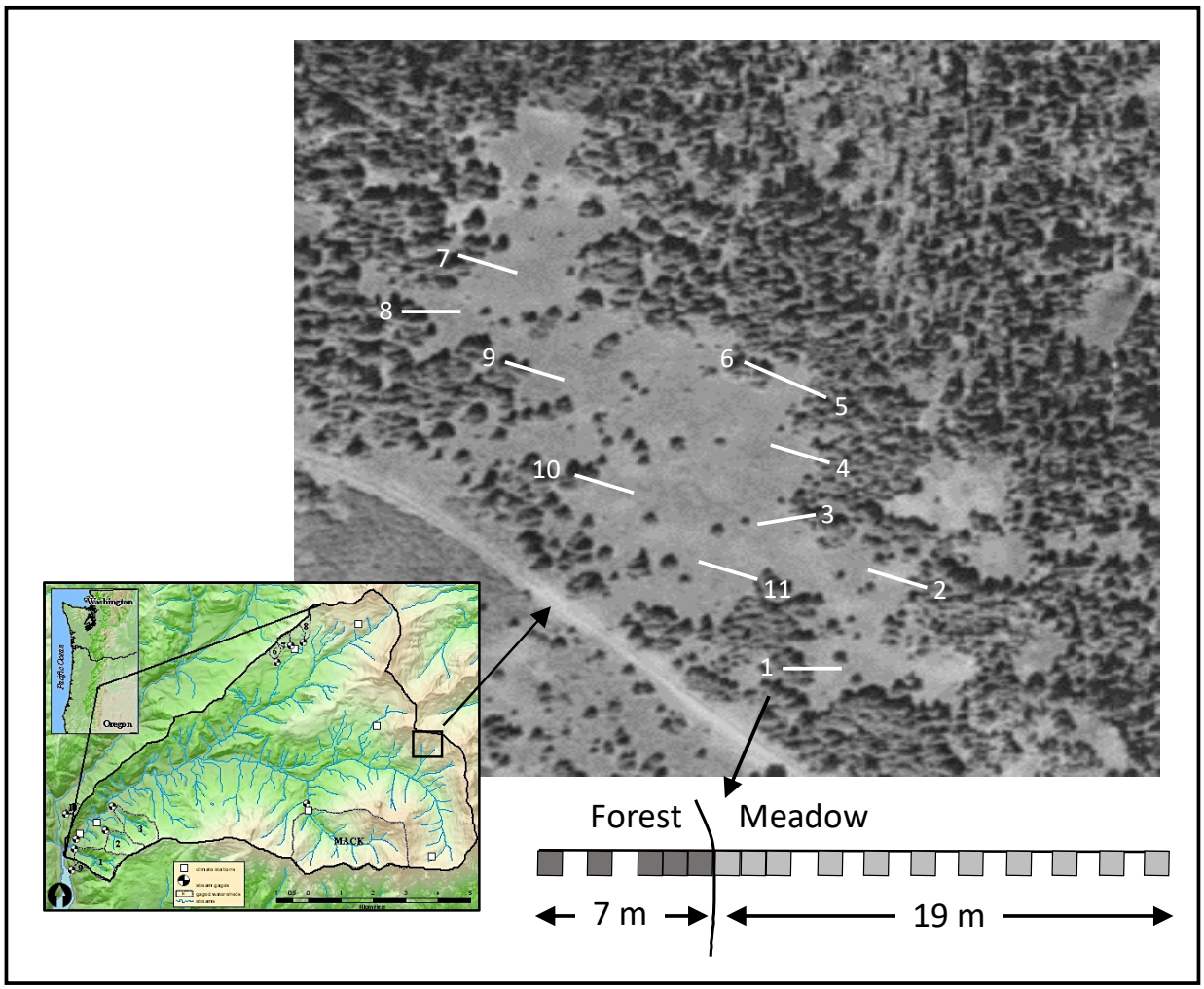
Online Resource 2. Location and aerial image of M1 on Frissell Ridge in the H. J. Andrews Experimental Forest, western Cascade Range, Oregon. The aerial photo shows the distribution of 26-m-long transects along east- or west-facing forest edges from lower- to upper-slope positions (bottom to top of photo). Transects 5 and 6 share an endpoint in open meadow. Each transect had 16, 1 × 1 m quadrats (5 in the forest, 11 in the meadow) in which we estimated species' cover, counted flowers or inflorescences, and measured light (% total transmitted light from a hemispherical photograph). Quadrat distance from edge was based on the drip line of the forest canopy (negative distances in the forest, positive distances in the meadow).



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Online Resource 3. Frequency (Freq.), cover, and density of flowering among species used to model relationships of flowering to light at Bunchgrass Ridge (BG).

		Abundance			Flowering		
Species	Inflor. type[a]	Freq. (%)	Median cover (%)	IQR[b]	Freq. (%)	Median density (no./m^2)	IQR[b]
Achillea millefolium	C	65.6	3.0	3.5	36.3	0.0	6.0
Fragaria virginiana	S	60.9	3.0	9.5	43.0	0.0	10.0
Erigeron aliceae	C	56.8	4.0	5.0	83.3	6.0	12.3
Cirsium remotifolium	C	55.4	4.0	6.0	60.7	4.0	14.0
Lupinus latifolius	S	48.0	5.0	8.5	62.0	8.0	76.0
Viola nuttallii	S	34.4	0.5	0.8	27.7	0.0	1.0
Iris chrysophylla	S	33.3	1.5	2.1	14.3	0.0	0.0
Phlox diffusa	S	32.0	9.5	24.3	69.1	31.5	88.0
Lathyrus nevadensis	S	26.5	3.0	3.5	12.8	0.0	0.0
Hieracium scouleri	C	24.8	3.0	5.0	72.6	15.0	53.0
Vicia americana	S	24.1	1.5	1.6	23.9	0.0	0.0
*Orthocarpus imbricatus**	C	19.7	1.5	1.9	100.0	16.0	24.0
Calochortus subalpinus	S	18.4	0.5	0.7	94.4	2.0	2.0
Symphotrichum spathulatum var. *spathulatum*	C	17.0	3.0	2.3	68.0	0.0	0.0
Agoseris aurantiaca	C	13.6	0.3	0.3	47.5	0.0	1.0
Eucephalus ledophyllus var. *ledophyllus*	C	10.5	2.0	2.5	32.2	0.0	3.5

Species present in at least 10% of quadrats are listed in descending frequency of occurrence. Asterisks indicate annuals. Abundance statistics are based on all quadrats (*n* = 294). Flowering statistics are based on quadrats in which a species was present (*n* varies by species). Plant nomenclature follows the USDA Plants Database (USDA and NRCS 2019).

[a] Inflorescence type: S = simple (single flower, raceme, or panicle); counts are of individual flowers. C = compound or complex/branching; counts are of inflorescences (multiple flowers).

[b] Interquartile range

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Online Resource 4. Frequency (Freq.), cover, and density of flowering among species used to model relationships of flowering to light at M1 (H. J. Andrews Experimental Forest).

		Abundance			Flowering		
Species	Inflor. type[a]	Freq. (%)	Median cover (%)	IQR[b]	Freq. (%)	Median density (no./m^2)	IQR[b]
Eriophyllum lanatum	C	70.6	7.0	8.0	82.4	17.0	37.3
Sanicula graveolens	C	58.2	12.0	24.0	15.7	0.0	0.0
*Microsteris gracilis**	S	47.7	1.0	0.5	95.9	7.0	9.0
Lupinus latifolius	S	44.4	4.0	5.0	5.9	0.0	0.0
Vicia americana	S	41.8	2.0	3.0	39.1	0.0	3.0
Achillea millefolium	C	39.2	3.8	6.6	33.3	0.0	7.0
*Collinsia parviflora**	S	37.9	1.0	1.5	94.8	30.0	49.8
Lathyrus nevadensis	S	33.3	4.0	4.5	64.7	3.0	12.5
*Orthocarpus imbricatus**	C	30.7	1.0	1.0	100.0	6.0	9.5
Ligusticum grayi	C	28.8	6.5	9.3	45.5	0.0	7.0
Cirsium remotifolium	C	28.1	3.0	2.5	48.8	0.0	6.5
Erigeron aliceae	C	27.5	6.5	11.1	73.8	6.0	22.0
Cerastium arvense	S	24.2	3.0	5.0	86.5	10.0	24.0
*Gilia capitata**	C	24.2	3.0	4.0	97.3	46.0	73.0
Penstemon procerus	S	22.2	4.5	8.0	35.3	0.0	25.3
Mimulus dentatus	S	21.6	5.0	6.0	75.8	5.0	10.0
Phlox diffusa	S	19.0	7.0	9.0	72.4	18.0	50.0
Potentilla gracilis	S	19.0	3.0	5.0	55.2	8.0	55.0
*Mimulus breweri**	S	18.3	1.0	0.5	96.4	20.0	34.5
Delphinium menziesii	S	17.0	1.0	0.5	92.3	7.0	7.0
Calochortus subalpinus	S	16.3	0.5	0	92.0	2.0	1.0
Lomatium martindalei	C	15.0	1.0	0	82.6	20.0	25.5
Castilleja hispida	C	14.4	0.5	0.5	59.1	1.0	1.8
Lomatium triternatum	C	13.7	1.0	0	76.2	11.0	17.0
Erysimum asperum	S	11.1	1.0	1.0	76.5	19.0	29.0
Potentilla glandulosa	S	10.5	6.5	10.0	43.8	0.0	17.0
Solidago canadensis	C	10.5	10.5	13.3	62.5	1.0	2.0

For details, see Online Resource 3.

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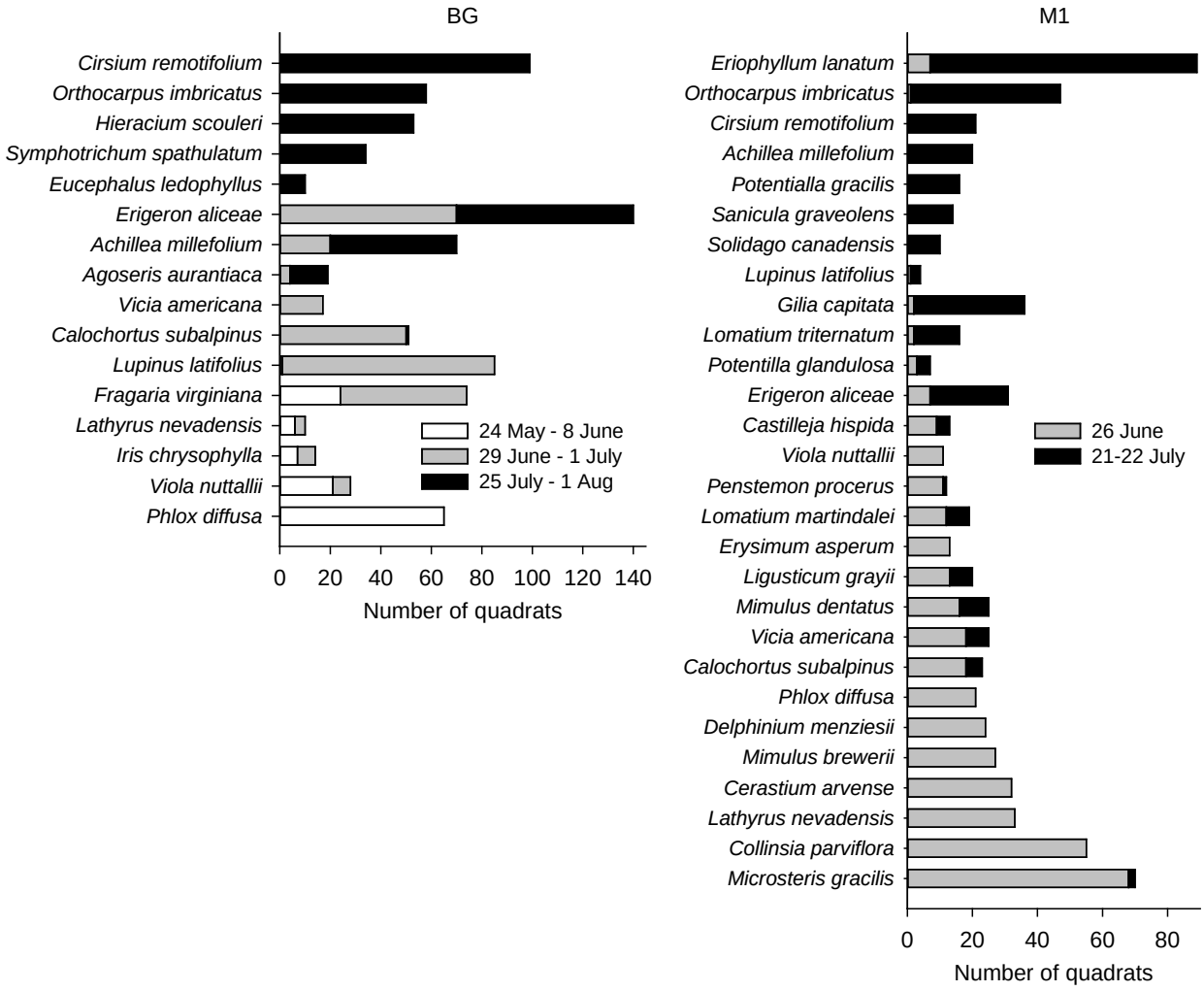
Online Resource 5. Distribution of peak flowering (maximum flowering density) among species at BG and M1. Flowering density was estimated at three points in the growing season at BG and twice at M1. Total bar length corresponds to the number of quadrats in which a species flowered (maximum of 294 at BG, 153 at M1). Shaded portions of bars correspond to the number of quadrats representing peak flowering for each sampling date. Species are arranged vertically by phenology of flowering (early to late from bottom to top).



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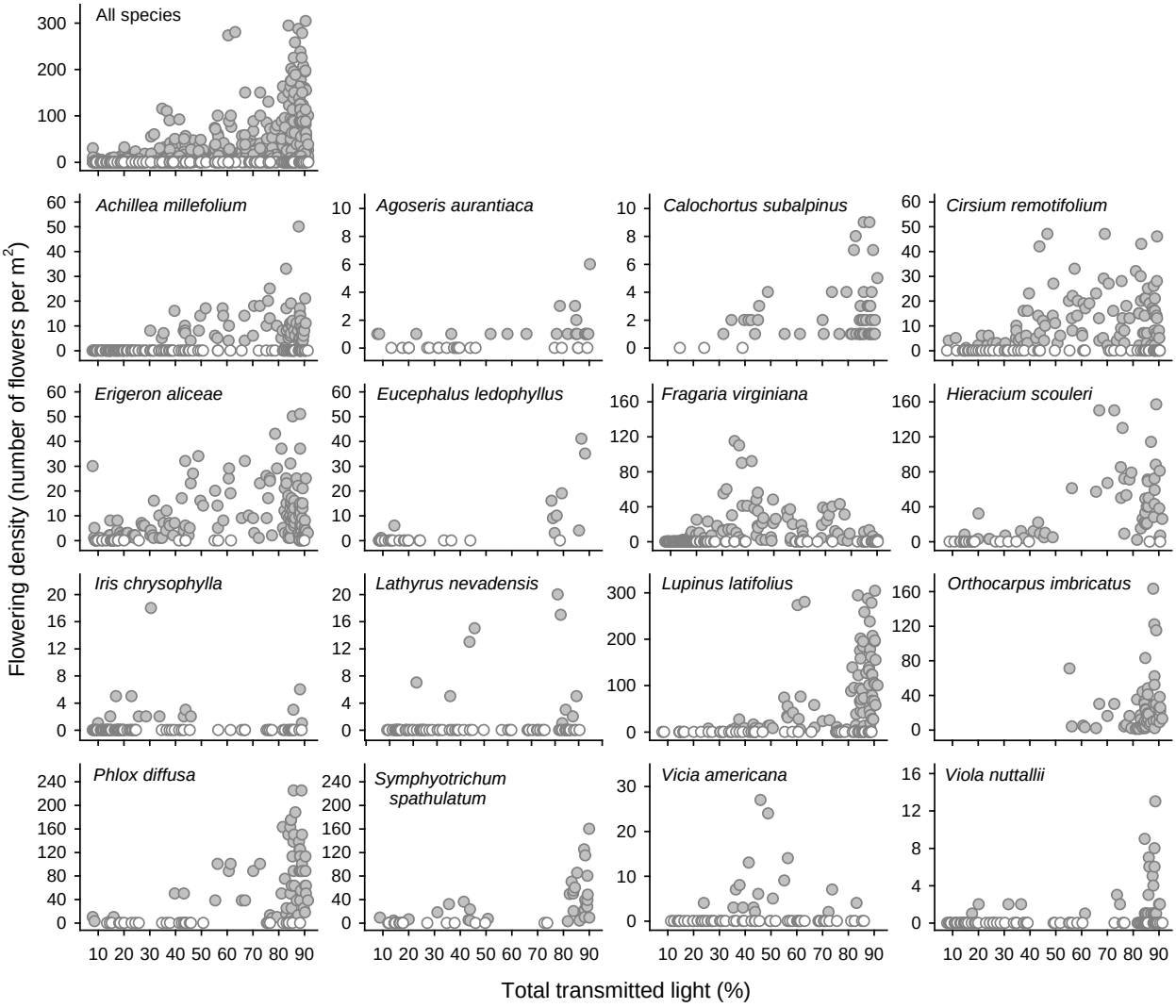
Online Resource 6. Flowering density (number of flowers or inflorescences per m^2) vs. total transmitted light (%) for the most common species at BG (those present in at least 10% of quadrats). See Fig. 4 for the corresponding plots of flowering effort**.**



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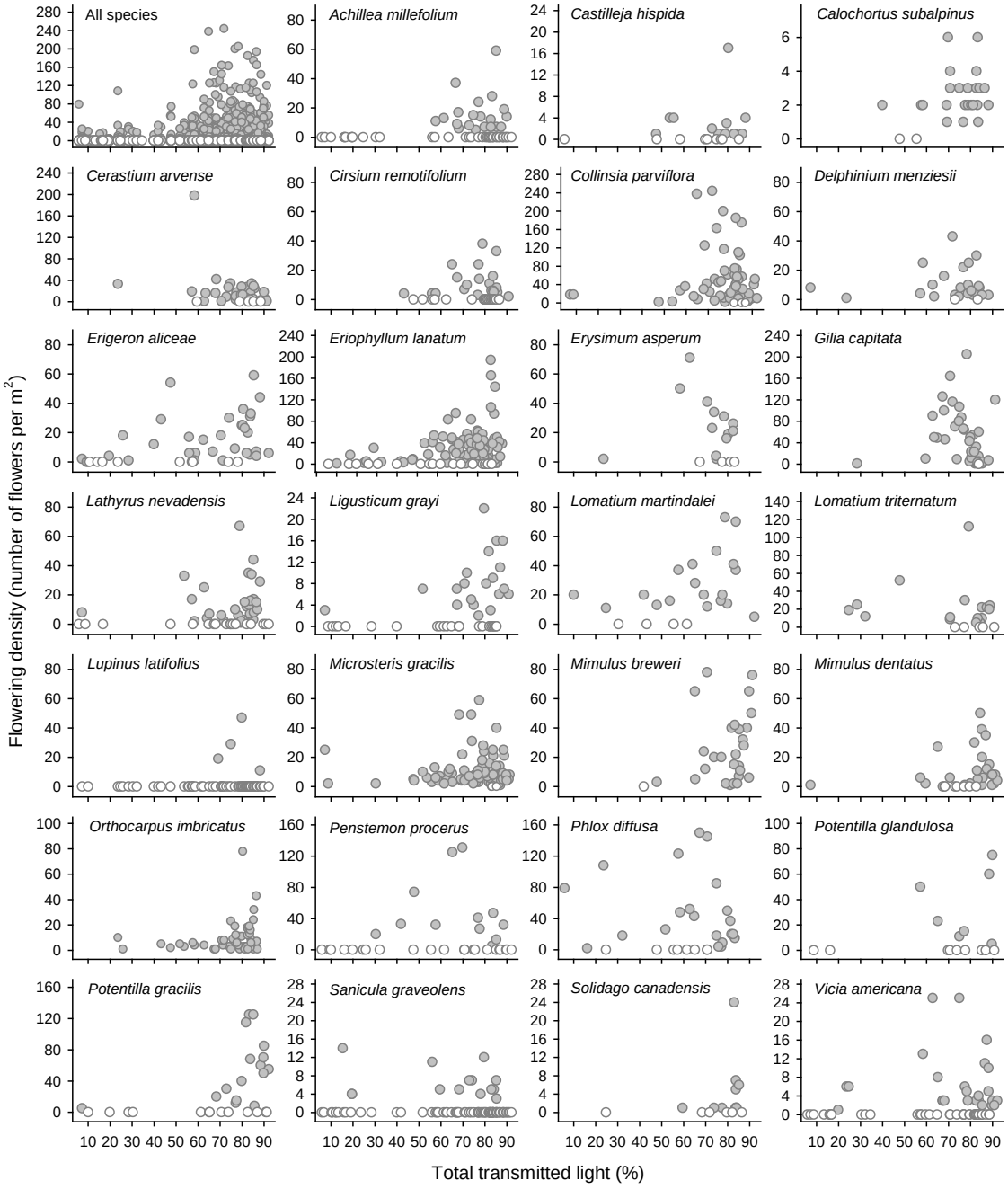
Online Resource 7. Flowering density (number of flowers or inflorescences per m^2) vs. total transmitted light (%) for the most common species at M1 (those present in at least 10% of quadrats). See Fig. 5 for the corresponding plots of flowering effort.