

Snowpack, fire, and forest disturbance: interactions affect montane invasions by non-native shrubs

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Abstract

Montane regions worldwide have experienced relatively low plant invasion rates, a trend attributed to increased climatic severity, low rates of disturbance, and reduced propagule pressure relative to lowlands. Manipulative experiments at elevations above the invasive range of non-native species can clarify the relative contributions of these mechanisms to montane invasion resistance, yet such experiments are rare. Furthermore, global climate change and land use changes are expected to cause decreases in snowpack and increases in disturbance by fire and forest thinning in montane forests. We examined the importance of these factors in limiting montane invasions using a field transplant experiment above the invasive range of two non-native lowland shrubs, Scotch broom (*Cytisus scoparius*) and Spanish broom (*Spartium junceum*), in the rain–snow transition zone of the Sierra Nevada of California. We tested the effects of canopy closure, prescribed fire, and winter snow depth on demographic transitions of each species. Establishment of both species was most likely at intermediate levels of canopy disturbance, but at this intermediate canopy level, snow depth had negative effects on winter survival of seedlings. We used matrix population models to show that an 86% reduction in winter snowfall would cause a 2.8-fold increase in population growth rates in Scotch broom and a 3.5-fold increase in Spanish broom. Fall prescribed fire increased germination rates, but decreased overall population growth rates by reducing plant survival. However, at longer fire return intervals, population recovery between fires is likely to keep growth rates high, especially under low snowpack conditions. Many treatment combinations had positive growth rates despite being above the current invasive range, indicating that propagule pressure, disturbance, and climate can all strongly affect plant invasions in montane regions. We conclude that projected reductions in winter snowpack and increases in forest disturbance are likely to increase the risk of invasion from lower elevations.

Keywords: climate change, fire, forest disturbance, interactions, invasibility, mountains, non-native plants, snowpack

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Introduction

Interactions between climate and disturbance regimes, and the complex effects these interactions can have on biodiversity and species distributions, remain a source of substantial uncertainty in forecasting future ecological change (Staudt *et al.*, 2013). Certain outcomes of global climate change are likely to be critical drivers of changes in vegetation, yet remain understudied; among these are winter warming and changes in forest disturbance rates (Kreyling, 2010; Grimm *et al.*, 2013a). In many temperate montane forests worldwide, these outcomes are likely to occur in the form of reduced winter snowpack at mid-elevations (Stewart, 2009), and in some cases such as the coniferous forests of western North America, increased frequency and/or severity of fires (Westerling *et al.*, 2006; Marshall *et al.*, 2008). The ultimate effects of these changes on plant species

distributions will also be influenced by land management decisions, further complicating our ability to predict future vegetation states (Grimm *et al.*, 2013b; Isabelle *et al.*, 2013; Staudinger *et al.*, 2013). For instance, cold-weather photoinhibition in plant leaves may be (Ball *et al.*, 1991) but is not necessarily (Blennow & Lindkvist, 2000) compounded by disturbances or management decisions which reduce insulation from forest canopy cover. Thus, the outcomes of winter warming and increased forest disturbance are likely to be complex. With changes in the winter environment predicted to occur more rapidly than changes during the growing season, understanding how winter warming interacts with other outcomes of global change is particularly urgent (Kreyling, 2010).

Mountainous regions are expected to be early bellwethers indicating plant species shifts in response to global change, because they are spatial compressions of relevant climatic gradients that exert strong influence on plant species distributions (Beckage *et al.*, 2008; Loarie *et al.*, 2009), provided that other factors that also

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vary with elevation do not also become limiting (Körner, 2012). There is increasing evidence of altitudinal range shifts by plant species in response to variation in temperature over the past century (Grabherr *et al.*, 1994; Kelly & Goulde, 2008; Gottfried *et al.*, 2012); however, there is less certainty regarding the role of winter snowpack in temperate mountain ranges in limiting the distribution of lowland plant species. In regions that generally experience subfreezing winter temperatures, snowpack can act to insulate plants from frost damage and permit low levels of metabolic activity and photosynthesis underneath snow (Starr & Oberbauer, 2003; Lundell *et al.*, 2010; Kreyling *et al.*, 2012; Pauli *et al.*, 2013). However, in regions where winter temperatures are milder and growth would otherwise be possible, snow cover is likely not beneficial to understory vegetation and can act to inhibit metabolic processes of plants that retain winter photosynthetic tissue (Barbour *et al.*, 1991; Saarinen *et al.*, 2011). Furthermore, general climate warming that causes less snow accumulation and earlier snowmelt may also make plants more tolerant of occasional freezing events (Loik *et al.*, 2004). Decreases in winter snowpack in response to climate change are expected to be greatest and most rapid around the elevation of the rain–snow transition zone in montane systems (Cayan *et al.*, 2008). Therefore, if lowland plants are sensitive to snowpack at these transition elevations where temperatures are milder than at high elevations, predicted future decreases in snowpack might trigger rapid range expansions of lowland plants through the transition zone.

Invasive, non-native species are often expected to be particularly responsive to changes in climate and disturbance regimes, due to traits such as high fecundity and dispersal rates, although evidence is mixed (Dukes & Mooney, 1999; Sorte *et al.*, 2013). In montane regions worldwide, there is a well-documented trend of fewer non-native plants with increasing elevation, which has been attributed to multiple mechanisms including increasing climatic severity, decreasing disturbance frequency, or decreasing propagule pressure with elevation (Pauchard *et al.*, 2009; Alexander *et al.*, 2011; Marini *et al.*, 2012). Observational evidence suggests that many successful montane invaders are cosmopolitan species that were initially introduced in adjacent lowlands, and therefore, propagule limitation is likely preventing the invasion of high-elevation specialists from other regions (Alexander *et al.*, 2011; McDougall *et al.*, 2011). However, such observational studies are not able to directly address the importance of increasing climatic severity or decreasing disturbance frequency in limiting the upslope spread of additional lowland invaders, beyond those cosmopolitan invaders that are presently found at higher elevations

(Alexander *et al.*, 2011; Seipel *et al.*, 2012), highlighting the importance of more in-depth research on invasion in model systems (Kueffer *et al.*, 2013). Experimental manipulations of invasive plants, especially transplant experiments beyond their current range limits, are therefore needed to differentiate the relative importance of climate, disturbance, propagule pressure, and their interactions, particularly in the context of climate change and increases in disturbance frequency (Pauchard *et al.*, 2009; Griffith & Loik, 2010; Ibáñez *et al.*, 2012).

In montane forests of western North America where snowpack is a dominant moisture reservoir, predicted decreases in snowpack depth and duration due to global climate change are likely to increase the frequency and severity of forest disturbance by fire, by reducing fuel moisture content and increasing flammability (Westerling *et al.*, 2006; Maurer, 2007; Lutz *et al.*, 2009). Many of these forests are also likely to experience increased disturbance from fuel-reduction thinning or commercial tree harvesting (Stevens *et al.*, 2014). Such disturbances can increase the pace of species range expansions in forests (De Frenne *et al.*, 2013), including by non-native species (Pauchard *et al.*, 2009). However, because snowpack may limit upslope invasion rates (Griffith & Loik, 2010), and snowpack has been shown to increase following forest disturbance (Musselman *et al.*, 2008; Molotch *et al.*, 2009), future reductions in snowpack caused by global climate change may accelerate upslope invasion rates by non-native plants into montane forests following disturbance.

We tested the effects of different snowpack–disturbance combinations on the population growth rates of two non-native shrubs in the family Fabaceae: Scotch broom (*Cytisus scoparius* (L.) Link.) and Spanish broom (*Spartium junceum* L.), both of which are invasive in the Sierra Nevada mountains of California, USA. We conducted a field transplant experiment above their current invasive elevation range, to test how specific demographic transition probabilities and population growth rate estimates responded to variation in winter snowpack, fire, and canopy closure. Snowpack duration has been previously shown to limit populations of some non-native plants at their upper elevation range margin (Ross *et al.*, 2008; Griffith & Loik, 2010), but the relative contributions of snowpack, fire, and canopy disturbance to invasion risk in montane forests have not been assessed. As both species are common disturbance colonizers that do not currently invade above the rain–snow transition zone, we predicted that population growth rates would increase with canopy disturbance and with the introduction of infrequent fire and would be greatest in disturbed forest under low winter snowpack levels. By planting this experiment slightly

above the current range of these species, where human population density is low, we also address the role of propagule limitation in determining their current distributions.

Materials and methods

Study species and location

Scotch broom and Spanish broom are shrub species native to Europe that are considered invasive noxious weeds in North America, including in the western foothills of the Sierra Nevada of California, where they can increase available soil N and compete with native tree seedlings for light and water (Bossard, 2000; Nilsen, 2000; Haubensak *et al.*, 2004). The two species share many ecological characteristics, although Scotch broom is much more extensively studied. Both species have thick seed coats and dormant seeds that persist in a soil seed bank for up to 20 years and can germinate at increased rates in response to fire, heat, and other soil disturbances (Bossard, 1991; Peterson & Prasad, 1998; Smith, 2000; Reyes & Traubad, 2009). Both species have photosynthetic stems that can fix carbon year-round and maintain a positive carbon balance even during winter months (Bossard & Rejmanek, 1992; Nilsen *et al.*, 1993). Both species can flower as early as the third growing season following germination, and viable seed production can exceed 10 000 seeds plant⁻¹ yr⁻¹ under favorable conditions (Bossard & Rejmanek, 1994; Rees & Paynter, 1997; Nilsen, 2000). Spanish broom, the species with the lower elevation invasive range in California and the more southerly native range in Europe, has greater water use efficiency and can assimilate a comparable amount of carbon within a shorter period of stomatal opening than Scotch broom (Nilsen *et al.*, 1993). We chose to study these species because their evergreen traits and potential for winter metabolism suggest that winter snow cover may limit their distribution. The upper elevation limit of invasive populations in this region is approximately 1000 m for Spanish broom and 1200 m for Scotch broom (J.T. Stevens, unpublished data), although scattered small populations of Scotch broom have been observed as high as 1510 m (Fig. 1). These range limits are roughly coincident with the occurrence of winter snowfall in the central Sierra Nevada, while the average freezing line of winter storms in this region ranges from approximately 1600 to 1800 m, above which snowfall is >50% of total annual precipitation (Barbour *et al.*, 1991; Lundquist *et al.*, 2008).

We conducted a field transplant experiment at the University of California Blodgett Forest Research Station in El Dorado County, CA (Fig. 1). Blodgett Forest (latitude 38°54'45"N, longitude 120°39'27"W) is located in the California mixed-conifer forest belt of the Sierra Nevada. Dominant canopy tree species include ponderosa pine (*Pinus ponderosa* Laws), sugar pine (*Pinus lambertiana* Dougl.), white fir (*Abies concolor* Gord. & Glend), incense-cedar (*Calocedrus decurrens* [Torr.] Floren.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and California black oak (*Quercus kelloggii* Newb.). Much of this forest type has been fire suppressed for over 100 years, but is actively managed for both timber harvesting and ecological

restoration using prescribed fire, leading to a range of canopy conditions (Collins *et al.*, 2007). Neither species is currently found at Blodgett Forest, although Scotch broom has been found on the forest in the past and is currently found on the main road leading up to Blodgett below approximately 1200 m asl (J.T. Stevens, unpublished data). This study was conducted between 1280 and 1340 m asl. Mean temperatures range from 0 to 8 °C in January and 10 to 29 °C in August. Mean annual precipitation is 160 cm, concentrated from October through April, and mean annual snowfall is 244 cm. Between 1990 and 1999, snowfall constituted an average of 22% of total precipitation (range 12–39%; all climate data courtesy F. Schurr).

Experimental design

We conducted a replicated split-plot experiment from September 2011 through June 2014, in which we sowed 2058 individually marked seeds of each species across 14 independent blocks to test the effects of canopy closure, snowpack, and fire. We tested the effect of canopy closure at the block level: Blocks were assigned to one of four classes of pre-existing canopy closure based on common forest management practices in Sierra Nevada forests to capture the full range of variation in canopy disturbance. Block locations were restricted to areas within the Experimental forest that could be accessed during the winter to conduct snow manipulations (an area within 1.5 km of the station headquarters, to which the road was plowed). Two blocks were in an 'Open' class, located in two different 2-ha group-selection harvests where all trees were removed within the previous 5 years. Two blocks each were located in a 'Closed' class and a 'Dense' class, each of which were unmanaged for approximately 100 years. Eight blocks were in a 'Thinned' class, located in stands where selected trees and surface fuel had been removed in by fuels treatments within the previous 10 years. The increased number of blocks in the Thinned class was to accommodate replicate prescribed fire treatments within this canopy class. The models we used to analyze our data are robust to this imbalance in sample size at the block level (Appendix S3; Pinheiro & Bates, 2000). In the open, closed, and dense canopy classes, the replicate blocks were in different management units and were spaced at least 0.4 km apart. Blocks in the Thinned canopy class were spread across three management units and were generally >0.2 km apart, with two exceptions. All blocks within a given canopy class had similar times since disturbance and similar vegetation structure and composition.

We measured percent light transmittance *T* at the center of each block with a canopy photograph taken with a Nikon 35-mm camera and a Nikkor fish-eye lens (8 mm f/2.8) placed 1 m aboveground. Color slides were converted to digital images that were analyzed with GLA software (Frazer *et al.*, 1999) to compute the percent of total transmitted photosynthetically active radiation. An analysis of variance indicated that classes were all significantly different from each other in canopy closure, defined as 100-*T* (Mean canopy closure in

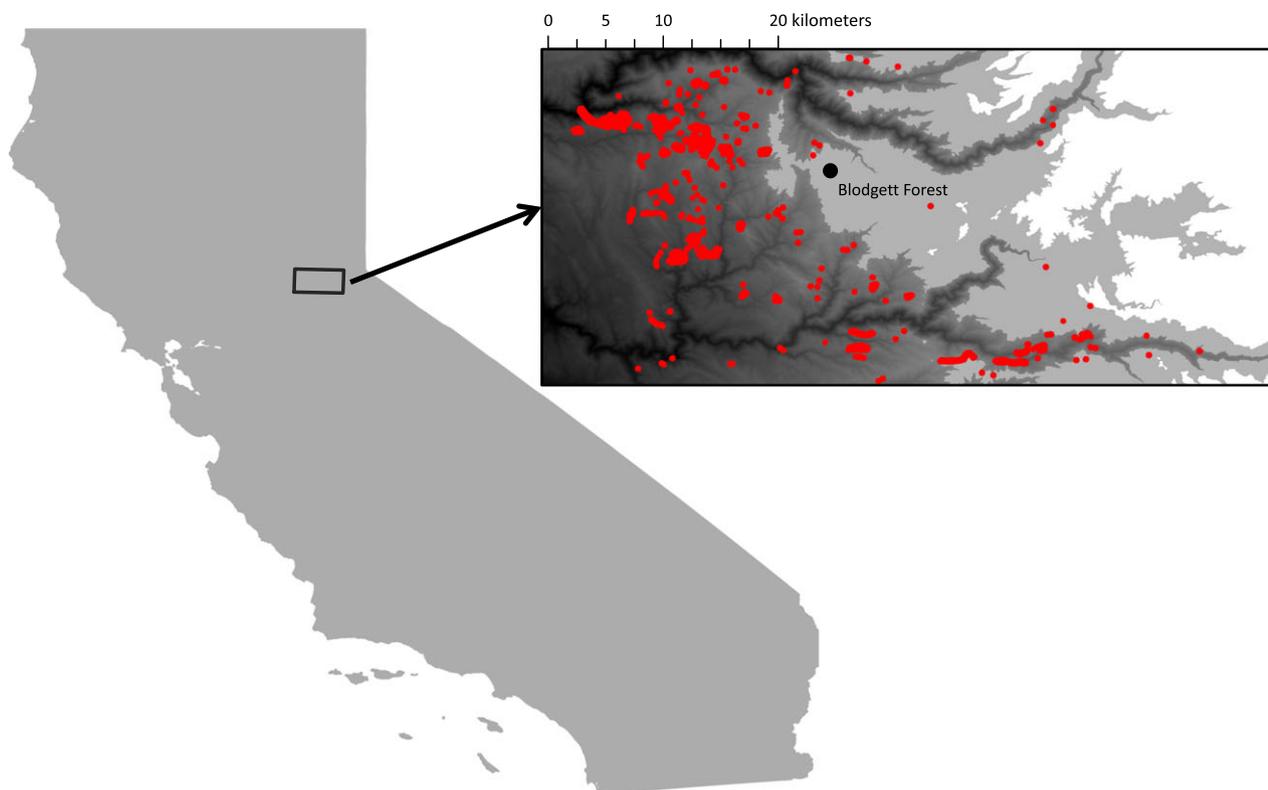


Fig. 1 Map of the study region. The study location of Blodgett Forest is shown. In the elevation relief map, the light gray band indicates 1220 m (4000 feet) elevation above sea level, and the white band indicates 1524 m (5000 feet) asl. Red points indicate known populations of Scotch broom, mapped by El Dorado National Forest (courtesy Matt Brown).

open = 14%, thinned = 59%, closed = 75%, dense = 85%; $F = 162.61$, $df = 3$, $P < 0.001$; for all pairwise comparisons, $P < 0.003$).

The fire treatments were also applied at the block level. Because of restrictions on burning, we were only able to apply fire within the Thinned stands, so we subdivided the increased number of blocks in the Thinned stands (8) into four blocks with no fire treatment and four blocks burned using light prescribed fire three weeks after planting, in October 2011. Ten-hour fuel moisture at the time of the burn was 8% and relative humidity was 45% with SW winds at 3 km h^{-1} , conditions typical of a fall prescribed burn in this region (R. York, personal communication). Fuel was added to the plots as necessary to create consistent fuel loads within and among blocks. Flame lengths were 1 m or less, and plots were left to smolder after the burn, with obvious visible fire effects and fuel consumption.

We split each $6 \times 3 \text{ m}$ block into three snowpack treatment units of $1.5 \times 3 \text{ m}$, which were separated from each other by a 0.5 m buffer. Each treatment unit received one of three winter snowpack levels (described below). Snowpack treatment units were randomly positioned within the block by a random draw of colored flags used to mark each treatment level. Within each snowpack treatment unit, we installed two 1 m^2 plots: one of Scotch broom and one of Spanish broom, which were randomly assigned within the treatment units by a blind

draw from a set of color-coded planter tags used to distinguish the two species. Each plot was cleared of duff and litter to expose bare mineral soil, and 49 seeds of the appropriate species were planted within a plot, in a 7×7 grid, at a depth of 2 cm which is optimal for Scotch broom germination (Bossard, 1993). Bossard (1991) found little evidence of seed predation on Scotch broom at a nearby site on Eldorado National Forest, particularly when seeds were buried. We marked each seed with a plastic planter stake to track the demography of individual plants, and no adults were present at this study site, so all plants that germinated were from our plantings. In blocks that were subsequently burned, litter and coarse woody debris were replaced onto the plots after planting to allow fire to burn through those plots, and seed locations were marked by steel nails. We measured the status (ungerminated/alive/dead) of all 4116 individuals at six time intervals. Initial fall germination immediately after planting was assessed in November 2011. Additional censuses occurred in May 2012, October 2012, May 2013, October 2013, March 2014, and June 2014 (to collect fecundity data). Germination was observed in November 2011, and each spring census, but no additional fall germination, was observed in 2012 or 2013. We counted predispersal seed set for all mature Scotch broom individuals in 2014, removing all fruits prior to maturity. We pulled all live plants and removed ungerminated seeds at the conclusion of the experiment by removing soil adjacent to the

planter stakes. The planter stakes remained in place for the duration of the experiment, and germination events were consistently adjacent to the planter stakes; thus, we were confident that there was little movement of seeds after planting and that all ungerminated seeds were removed.

During the winter, snowpack manipulations occurred within two days after every storm that produced at least 15.2 cm (6 inches) of snow. Snowpack treatments were reduced, ambient, and increased snowpack levels. Snow was manually shoveled off reduced-snow treatment units until approximately 50% of ambient snow depth was covering the treatment unit, and gently shoveled onto increased-snow treatment units to minimize snow compaction, until approximately 200% of ambient snow depth was covering the treatment unit. Snowfall varied among both canopy classes and years (Table S1), with total accumulation highest in open canopy blocks during 2011–2012 (average snowfall 212.1 cm), and lowest in dense canopy blocks during 2013–2014 (average snowfall 7.6 cm) (Table S1; F. Schurr, personal communication). We measured soil temperature and volumetric water content at one of the thinned blocks from 2011 to 2012 using ECh2O 5TM probes (Decagon Devices Inc., Pullman, WA, USA) at a depth of 0–5 cm. Snowpack manipulations affected the duration of snow cover, as evidenced by daily fluctuations in temperature during snow-free periods (Fig. S1). Winter temperatures at this block never dropped below 0 during snow-free periods, confirming a relatively mild winter climate in the rain–snow transition zone. Because snow totals varied among canopy classes and years, we treated snow depth as a continuous variable rather than as a categorical variable. After treatment, we measured snow depth in each snowpack treatment unit. For small storms where <15.2 cm of snow fell and no manipulations were conducted, we estimated the additional snow totals per storm at each block. We first calculated the average ratio of measured ambient snowfall after large storms at a given block to snowfall after the same large storms at the Blodgett Forest meteorological station, which records snowfall on a daily basis. We then multiplied this block-specific ratio by the snowfall total at the meteorological station for each small storm and added these additional snow totals to the measured postmanipulation totals, to estimate a full-season snowfall total for each snowpack treatment within each block. We used these estimated full-season totals in our analyses.

Data analysis

Our objectives were to determine the effects of our experimental treatments on broom populations at specific life stages and to compare estimates of population growth rate among different global change scenarios, for each species. To do this, we used logistic regression models to explicitly quantify the relationship between specific life-stage transition probabilities and the canopy, fire, and snowpack factors we manipulated in this experiment (Appendix S3). We then used the transition probability estimates, and the statistical uncertainty associated with these estimates, to parameterize Leslie population projection matrices for

fifteen global change scenarios, representing five combinations of canopy closure and fire (open, thinned + unburned, thinned + burned, closed, and dense), at three annual snowfall levels. The block-level uncertainty in our model estimates is somewhat imprecise because of the low replication in three canopy classes; however, the among-block variance in most transition probabilities was less than or comparable to the average within-plot variances in a given canopy class (Appendix S3).

We chose to use regression models to estimate transition probabilities, rather than use observed transition probabilities from different treatment combinations and then estimate which transition probabilities were sensitive to treatment effects (e.g. a life table response experiment; Caswell, 1989; Angert, 2006), because the use of regression models allows us to quantify the direct relationship between explanatory variables and each transition probability by modeling the successful transition of each individual as a binomial process (Besbeas *et al.*, 2009). This approach is commonly used in integral projection models, which describe growth over discrete time of populations structured by a continuous state variable (Jacquemyn *et al.*, 2010; Rees *et al.*, 2014). We were interested in population growth responses to annual snowfall as a continuous variable; however, life table response experiments are not well equipped to model the response of population growth to variation in continuous (rather than discrete) environmental conditions (Gotelli & Ellison, 2006). Furthermore, stage-structured matrix population models must have the same projection interval (i.e. time step) for each transition probability contained within the projection matrix (Caswell, 2001). By estimating transition probabilities using logistic regression, different interval estimates can be combined into a common time step (Besbeas *et al.*, 2009). This allowed us to define probability estimates for some transitions at subannual time intervals, for instance, to separate the effects of snowpack on summer vs. winter survival of seedlings at approximately six-month intervals. We thus distinguish between *component probabilities*, which occur at subannual time intervals and were modeled using logistic regression, and *annual transition probabilities*, which can be the product of several component probabilities and are used to populate the population projection matrix and calculate the population growth rate (Table 1). The hierarchical statistical models used to describe the relationship between environmental variables and component probabilities are given in Appendix S3.

In cases where relevant transitions continued to occur outside of the three-year scope of this study (e.g. continued dormancy and reproduction beyond three years, and adult survival), we derived the relevant component probabilities using a combination of existing data and published estimates. At the beginning of the seed bank period, which we defined as extending from the beginning of the third potential growing season indeterminately into the future (Fig. 2), the probability of returning dormant to the seed bank (PdB ; Table 1) depended on whether the seeds had previously been burned by prescribed fire. For seeds in burned plots, we set $PdB = PgB/Pg2$, in other words, the rate of decline in

Table 1 Calculation of annual transition probabilities used in the matrix projection model, based on component probabilities estimated from regression of experimental data, from sampling nearby populations, or from published estimates

Description	Annual transition probability	Formula from component probabilities*
Probability of dormancy in year 2	$Pd2$	$1 - Pg2$
Probability of dormancy in seed bank (year 3 and beyond)	PdB	PdB
Probability of a first-year seedling establishing from a 1st-year dormant seed	$Ps1y1$	$Pg2 * Pss1$
Probability of a first-year seedling establishing from a seed-bank seed	$PsBy1$	$PgB * Pss1$
Probability of a first-year seedling surviving to become a second-year seedling	$Py1y2$	$Pws1 * Pss2$
Probability of a second-year seedling surviving to become a pre-adult	$Py2pa$	$Pws2 * Pss2 * (1 - Pm3)$
Probability of a second-year seedling surviving to become an adult	$Py2a$	$Pws2 * Pss2 * Pm3$
Probability of a pre-adult surviving to the next year	Ppa	Ppa
Probability of maturity of a pre-adult	$Pmpa$	$Pmpa$
Number of first-year dormant seeds per adult	Nas	$S * Pd1$ [$Pd1 = 1 - Pg0 - Pg1$]
Number of just-dropped adult seeds establishing as first-year seedlings in year $t + 1$, per adult	$Nasdlg$	$S * ((Pg0 * Pws0 * Pss1) + (Pg1 * Pss1))$
Probability of adult survival	Pa	Pa

*Component probabilities are as follows: first fall germination after dispersal ($Pg0$), first spring germination ($Pg1$), second spring germination ($Pg2$), germination from the seed bank in year 3 and beyond (PgB), winter survival immediately after fall germination ($Pws0$; Spanish broom only), first-summer survival ($Pss1$), first winter survival ($Pws1$), second summer survival ($Pss2$), second winter survival ($Pws2$), seed set (S), and the probability that a plant in its second growing season reaches reproductive maturity by the end of its third growing season ($Pm3$).

germination from the second spring to the third spring. For seeds in unburned plots, we set $PdB = 0.68$, an estimate of Scotch broom seed bank germination following moderate

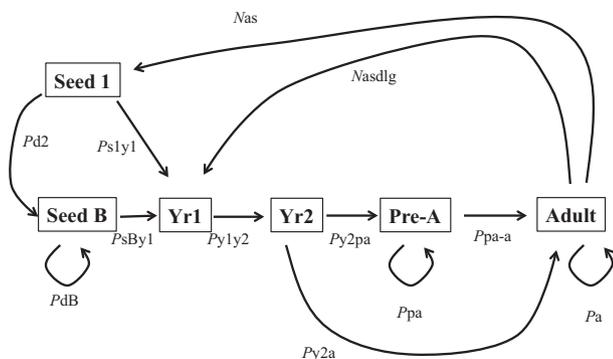


Fig. 2 Stage-structured life cycle diagram for both broom species, showing annual transition probabilities (P) and reproductive contributions (N). Transitions between stages (shown in boxes) occur at the onset of seed dispersal (late summer) and reflect the presence of seed dormancy in the first year after dispersal (Seed 1) and in the seed bank (Seed B). Seedlings at the end of their first and second summer (Yr 1) transition to seedlings at the end of their second summer (Yr 2) and then can transition to either pre-adults (Pre-A) that continue vegetative growth, or directly to reproductive adults (Adult) in the third growing season. Annual transition probabilities and reproductive contributions in many cases represent the product of subannual component probabilities that are specific to germination and/or seasonal survival (Table 1).

severity wildfire in a nearby region of California where subsequent burns did not stimulate additional germination (Hauensak *et al.*, 2004).

We statistically modeled the probability that a live plant during its third growing season would be reproductively mature, $Pm3$ (Table 1), using the binomial regression approach (Appendix S3) for Scotch broom only, because Spanish broom did not flower during the third growing season. For Scotch broom pre-adults (immature individuals in the third growing season and beyond), we derived the annual probability of subsequent maturity $Pmpa$ by setting $Pmpa = Pm3$ for the two canopy classes (open and thinned) for which we had flowering data in year 3. We set $Pmpa = 0.075$ for the Closed and Dense canopy classes, which was the modeled value of $Pm3$ from the Thinned canopy class. In these two canopy classes, the height of the largest surviving plants in year 3 (range 43–55 cm) was comparable to the mean height in year 2 of those plants that flowered in year 3 ($64.7 \text{ cm} \pm 5.7 \text{ cm}$). We calculated the probability of annual survival for both pre-adults (Ppa) and adults (Pa) as the maximum block-level survival rate for a given species from the second growing season to the third growing season (0.80), across all scenarios. Finally, we statistically modeled individual seed output S using pre-dispersal seed set from Scotch broom. S was modeled as a function of canopy, fire, and snow treatments, using the regression approach described in Appendix S3 modified for count data using a Poisson distribution. Because there were no mature individuals in the Closed or Dense canopy classes in year 3, we set the putative value for S for future mature individuals equal to the lowest modeled value of S from the data ($S = 64$). Although we lacked flowering data on Spanish

broom, because the heights of surviving individuals were comparable to Scotch broom, and because this species is ecologically similar to Scotch broom (Zouhar, 2005), we set all reproductive parameters for Spanish broom equal to those for Scotch broom with the exception of $Pm3$, which was 0.

Having assigned fixed values or parameter distributions to all component probabilities and calculated the resulting annual transition probabilities (Table 1), we defined a stage-structured population projection matrix based on the life stages described in Fig. 2 (Caswell, 2001). The simulated annual cycle started in late summer (approximately September 1), with the dispersal of seeds from the adult population, and subsequent stage transitions represent the period from seed dispersal in year t through summer survival in year $t + 1$, encompassing a putative growing season from approximately March through July. Our population projection matrix included six stages (Fig. 2, Table S2): Seed 1 (dormant seed after growing season 1), Seed B (dormant seed after growing season 2, in the seed bank), Yr 1 (1-year-old seedling), Yr 2 (2-year-old seedling), Pre-A (pre-adult in its third year and beyond), and A (adult having reached reproductive maturity).

To investigate how interactions between snowpack and canopy closure influence population growth rate λ , we estimated λ by calculating the dominant eigenvalue for population projection matrices for each of 12 scenarios (4 canopy classes \times 3 annual snowfall totals). Although the average winter snowfall at Blodgett Forest is 244 cm, the three years from 2012 to 2014 were all below-average snowfall years in the Sierra Nevada, with the highest snowfall total in 2012 at only 212 cm (Table S1). We therefore chose to estimate component probabilities for three discrete annual snowfall scenarios of 25, 100, and 175 cm, to constrain our model predictions within the range of observed snowfall totals. To integrate the parameter uncertainty from the component models into the demographic model and produce distributions of estimated population growth rates, each matrix A was derived by independently sampling the parameters for all model-estimated component probabilities and calculating the resulting annual transition probabilities described in Table 1 1000 times. Each sampled component probability was defined as the inverse logit of a random draw from a normal distribution with mean β and standard deviation σ , based on best model fits from the logistic regressions in Appendix S3. The parameters β and σ were selected from the highest-level model with support based on AIC_c values, with the model hierarchy increasing from a null model to a canopy closure model to a snowpack model nested within a given canopy class (Tables 1 and 2). We evaluated the contribution of each annual transition probability to λ using sensitivity and elasticity values for each scenario (Caswell, 2001), which we calculated using a population projection matrix derived from the mean value of each component probability for each scenario.

To investigate how interactions between fire and snowpack influence λ within the Thinned canopy class, we defined two population projection matrices for each simulated snowfall level: one burned (A_B) and one unburned (A_{UB}), using the equivalent matrix parameterization as the Thinned canopy class (described above). For A_B , we used germination

probabilities from the best model fits estimated by our logistic regressions for each species (Tables 1 and 2). Based on published data for Scotch broom, we assumed complete seedling mortality in the first two seedling stages (Agee, 1996), and 13% survivorship of the adult and pre-adult stages (Tveten & Fonda, 1999) following fire. Because little is known about Spanish broom responses to fire at the seedling and adult stages (Zouhar, 2005), we used the same live-plant response estimates as for Scotch broom. We assumed that fires were of a similar type to that used in our experiment: a low-severity surface fire conducted after the period of seed dispersal (September 1). To model the effects of fire on λ at different return intervals, we used periodic matrix models (Caswell, 2001) for a series of fixed fire return intervals i ranging from 1 to 50 years. We defined the periodic matrix A_p as a matrix multiplication product of $i - 1$ identical unburned matrices followed by one burned matrix, thus initiating the periodic matrix with a fire year: $A_p = A_{UB}[i-1] * A_{UB}[i-2] * \dots * A_{UB}[1] * A_B$ (Hoffmann, 1999). Because germination effects already account for differential effects of fire on just-dispersed, 1-, 2-, and >2-year dormant seeds, and live plants have a priori defined mortality rates, a single burned matrix accounts for potential lags in fire effects; therefore, the following year should resume unburned transition rates. The annual estimate of λ is then simply the i th root of A_p (Hoffmann, 1999). By simulating 1000 iterations of A for each snowfall–fire combination described above, we obtained a mean and standard deviation estimate for λ at each value of i .

Results

Demographic vital rates of both broom species responded to strong interactions between canopy closure, snowpack, and prescribed fire. In general, the two species responded similarly; however, different global change factors were most relevant at different life stages. For instance, canopy closure exerted strong influence on the germination phase of both species, but had less effect once plants were alive (Table 2). For each species, germination probability was highest in the thinned canopy class, and lowest in either the open or dense canopy class. This trend also held across all germination stages, from initial fall germination to germination from the seed bank. Model comparison using ΔAIC_c indicated that models accounting for canopy class had substantially more support than null models for all germination stages, except initial fall germination of Scotch broom, which had a very small sample size ($n = 27$ fall germinants). The only other life stages for which canopy class played an important role were survival during the first summer, probability of maturity in year 3, and seed set (Table 2). For each species, first-summer survival was greatest in the thinned canopy class and lowest in the dense canopy class; summer survival probabilities were higher overall for Scotch broom than for Spanish broom (Table 2). Scotch broom

Table 2 Modeled component probability estimates across different canopy classes and fire classes, for Scotch broom (a) and Spanish broom (b)

Component probability*	Canopy†				Fire‡			
	ΔAICc	β (σ)				ΔAICc	β (σ)	
		O	T	C	D		T-UB	T-B
(a)								
<i>Pg0</i>	-0.876	-4.32 (0.19)	-4.32 (0.19)	-4.32 (0.19)	-20 (0)	-3.529	-4.06 (0.23)	-4.06 (0.23)
<i>Pg1</i>	33.187	-2.16 (0.19)	-1.37 (0.07)	-1.54 (0.16)	-2.56 (0.23)	28.007	-1.85 (0.12)	-1.00 (0.15)
<i>Pg2</i>	132.497	-2.04 (0.19)	-1.15 (0.08)	-2.02 (0.20)	-20 (0)	-1.029	-1.15 (0.08)	-1.15 (0.08)
<i>PgB</i>	20.74	-23 (0)	-3.18 (0.19)	-3.72 (0.45)	-23 (0)	-2.98	-3.18 (0.19)	-3.18 (0.19)
<i>Pss1</i>	12.38	-0.24 (0.26)	0.92 (0.11)	0.90 (0.25)	-0.29 (0.45)	-0.63	0.92 (0.11)	0.92 (0.11)
<i>Pws1</i>	-8.01	1.19 (0.11)	1.19 (0.11)	1.19 (0.11)	1.19 (0.11)	-3.55	1.26 (0.13)	1.26 (0.13)
<i>Pss2</i>	-8.05	1.36 (0.19)	1.36 (0.19)	1.36 (0.19)	1.36 (0.19)	-3.23	1.39 (0.23)	1.39 (0.23)
<i>Pws2</i>	-10.37	1.58 (0.21)	1.58 (0.21)	1.58 (0.21)	1.58 (0.21)	-3.68	1.56 (0.25)	1.56 (0.25)
<i>Pm3</i>	21.92	1.39 (0.80)	-2.51 (0.43)	-20 (0)	-20 (0)	0.31	-2.51 (0.43)	-2.51 (0.43)
<i>S</i>	299.29	5.08 (0.03)	4.15 (0.05)	-20 (0)	-20 (0)	-3.90	4.15 (0.05)	4.15 (0.05)
(b)								
<i>Pg0</i>	38.097	-3.87 (0.41)	-2.00 (0.09)	-2.33 (0.21)	-3.25 (0.30)	-0.481	-2.00 (0.09)	-2.00 (0.09)
<i>Pg1</i>	17.635	-3.05 (0.28)	-1.98 (0.10)	-2.32 (0.21)	-3.03 (0.28)	3.611	-2.26 (0.15)	-1.74 (0.19)
<i>Pg2</i>	62.212	-4.51 (0.58)	-2.06 (0.11)	-2.96 (0.29)	-4.90 (0.72)	4.911	-1.80 (0.13)	-2.43 (0.22)
<i>PgB</i>	7.835	-5.60 (1.00)	-3.33 (0.19)	-3.82 (0.45)	-5.59 (1.00)	-3.256	-3.33 (0.19)	-3.33 (0.19)
<i>Pws0</i>	-6.74	1.41 (0.18)	1.41 (0.18)	1.41 (0.18)	1.41 (0.18)	-3.135	1.41 (0.18)	1.41 (0.18)
<i>Pss1</i>	18.386	-1.39 (0.63)	0.76 (0.15)	0.11 (0.33)	-1.79 (0.76)	-0.396	0.76 (0.15)	0.76 (0.15)
<i>Pws1</i>	-2.73	-0.95 (0.16)	-0.95 (0.16)	-0.95 (0.16)	-0.95 (0.16)	-2.67	1.09 (0.18)	1.09 (0.18)
<i>Pss2</i>	-1.58	-1.40 (0.22)	-1.40 (0.22)	-1.40 (0.22)	-1.40 (0.22)	-2.74	1.63 (0.25)	1.63 (0.25)
<i>Pws2</i>	-6.79	1.63 (0.22)	1.63 (0.22)	1.63 (0.22)	1.63 (0.22)	-3.72	1.59 (0.24)	1.59 (0.24)

β parameters describe maximum likelihood estimates of component probabilities on a logit ($\log[P/(1-P)]$) scale. Estimates of β and σ come from binomial models in Appendix S3 Eq. 1, with parameters on a logit scale, except for *S*, which comes from a poisson model with parameters on a log scale. ΔAICc values are for the model of interest (canopy or fire) minus a null model without the term of interest. Bold font indicates parameters that were selected for the demographic model.

*Component probabilities are as follows: first fall germination after dispersal (*Pg0*), first spring germination (*Pg1*), second spring germination (*Pg2*), germination from the seed bank in year 3 and beyond (*PgB*), winter survival immediately after fall germination (*Pws0*; Spanish broom only), first-summer survival (*Pss1*), first winter survival (*Pws1*), second summer survival (*Pss2*), second winter survival (*Pws2*), and third-year maturity (*Pm3*; Scotch broom only). *S* is the parameter for number of seeds produced by flowering adults in their third year, on a log scale. Spanish broom did not flower in year 3.

†Canopy classes are open (O), thinned (T), closed (C), and dense (D).

‡Fire classes are Unburned (UB) and Burned (B), both were applied only within the thinned canopy class.

had a higher 3rd year maturity rate and a higher seed set in the open canopy class, and no individuals reached maturity in the closed or dense classes. Like canopy closure, fire also primarily influenced the germination stages. For both species, fire was associated with higher germination rates during the first spring germination stage (Table 2). For Scotch broom, no other germination stage was affected by fire. However, Spanish broom had a greater second spring germination probability in unburned plots relative to burned plots (Table 2b).

When snowpack models were supported for a particular component probability, estimated total winter snowfall always had a negative effect, regardless of species, although the life stages at which snowpack

was important varied by species, canopy class, and fire occurrence (Table 3). In the thinned canopy class, total winter snowfall had a negative effect on winter survival probabilities (Table 3). This effect was observed in the first winter for both species and strongly in all winters for Spanish broom. Also for both species, the negative effect of snowpack on survival applied to both burned and unburned plots within the thinned canopy class (Table 3). For other canopy classes, there was no detectable effect of snowpack on winter survival, although the parameter estimates tended to indicate a negative effect. Standard deviations of the parameter estimates for these other canopy classes were generally high, suggesting that the small sample sizes in these classes due to their low germination rates relative to the thinned

canopy class kept confidence in model estimates low. However, we did detect a weak negative effect of snowpack on first spring germination probability in the densely shaded canopy class for Scotch broom. Lastly, for Scotch broom, we detected a negative effect of snowpack on first-summer survival within the thinned canopy class, although the snowpack model was only supported for unburned plots (Table 3).

Population projections under most climate–disturbance scenarios suggest that populations of both Scotch broom and Spanish broom would be expected to increase ($\lambda > 1$) under most conditions, under the parameters used in this model (Fig. 3). The mean estimate of lambda for Scotch broom was greater than 1 for all scenarios except for high annual snowfall in thinned plots ($\lambda = 0.88$) and dense plots ($\lambda = 0.92$) and was highest in open canopy plots ($\lambda = 1.91$). The mean estimate of lambda for Spanish broom was greater than 1 for all scenarios except for thinned plots with moderate annual snowfall ($\lambda = 0.80$) and high annual snowfall ($\lambda = 0.81$), while the highest estimate of lambda was in the thinned plots with low annual snowfall ($\lambda = 2.13$). The thinned canopy class also had the greatest range of λ , attributable to the strong effects of snowpack in this canopy class (Fig. 3). The elasticity scores within the thinned canopy class indicate that the importance of early life-stage transitions (e.g. seedling survival) to λ decrease with increasing snowfall totals, while the importance of later life-stage transitions (e.g. adult survival) increases with snowfall (Table S4.3). Population growth rates in most other canopy classes were not responsive to variation in snowpack (Fig. 3), as the statistical models in those classes lacked strong support for a snowpack effect, with the exception of the dense canopy class for Scotch broom (Table 3).

The occurrence of frequent fire reduced λ in both species despite positive effects on germination (Table 3), because of high expected mortality of seedlings and adults (Agee, 1996; Tveten & Fonda, 1999). As fire return interval (FRI) increased, estimates of λ approached the estimates derived from unburned stands (Fig. 4). We observed an interaction between fire and snowpack for both species, where the rate of increase in λ with increasing FRI depended on the expected snowpack level (Fig. 4). For some snowfall scenarios, the fire return interval affected the likelihood of population growth vs decline. For instance, under an intermediate snowfall level of 100 cm, the mean population growth rate estimate for Scotch broom was positive ($\lambda > 1$) with an FRI > 8 years, while the mean population growth rate for Spanish broom was within 1 standard deviation of $\lambda = 1$ with an FRI > 19 years (Fig. 4). Thus, if moderate-to-high snowpack levels depress population growth rates to levels near 1, the

frequency of fire can play a role in population spread, while if low snowpack promotes rapid population growth, fire frequency may have little impact on spread (Fig. 4).

Discussion

We found support for the theory that montane plant invasions are limited by a combination of winter climate, disturbance rates, and propagule pressure (sensu Pauchard *et al.*, 2009). In particular, projected decreases in winter snowpack caused by global climate change may facilitate the spread of invasive lowland plants to higher elevations. We demonstrate that demographic transitions between early life history stages play an important role in determining population responses to winter climate variation (Appendix S4; Rees & Paynter, 1997; Neubert & Parker, 2004), highlighting the importance of manipulative experiments that measure responses of early life stages to a range of possible global change outcomes (Shevtsova *et al.*, 2009). We found strong interactive effects between winter climate and canopy disturbance in determining the magnitude of λ , suggesting that climate and disturbance can both strongly influence the rate of invasion at high elevations (Pauchard *et al.*, 2009). However, by planting invasive species above their invasive range and finding positive population growth rates, we also show that propagule limitation of lowland invaders likely plays a role in determining current altitudinal invasion extents in montane regions (Alexander *et al.*, 2011). Estimates of population growth rate (λ) were greater than 1 for many combinations of snowpack, fire, and canopy closure, with high confidence (Figs 3 and 4), indicating that non-native brooms are able to sustain populations across a wide range of environmental conditions (Parker, 2000).

Our methodological approach of modeling component transition probabilities at subannual intervals revealed in more detail the mechanisms driving population trends. For both species, the strongest negative effect of snowfall was observed during winter survival of seedling stages, particularly during the first winter after germination (Table 3). This suggests that either prolonged frost injury or physical injury under deeper snowpack is largely responsible for declines in population growth rates. However, these broom species are known to fix carbon and nitrogen over the winter months (Wheeler *et al.*, 1979; Nilsen *et al.*, 1993) and therefore may take advantage of a longer growing season under low snowpack conditions to build up root biomass and carbon stores, particularly when ambient winter air temperatures are often above freezing, as they are in the Sierra Nevada transition zone. We found

Table 3 Modeled effect sizes of total winter snow accumulation on each subannual transition probability, for Scotch broom (a) and Spanish broom (b)

Component probability*	open		thinned– unburned		thinned–burned		closed		dense	
	ΔAICc	β	ΔAICc	β	ΔAICc	β	ΔAICc	β	ΔAICc	β
(a)										
<i>Pg1</i>										
Estimate	–2.00	0.001	–1.17	–0.002	–1.99	0.0002	–1.78	0.0006	2.48	–0.021
σ		0.002		0.002		0.002		0.003		0.008
<i>Pg2</i>										
Estimate	1.22	0.007	–0.27	0.006	–1.13	0.006	–2.06	0.0002	NA	NA
σ		0.004		0.005		0.006		0.014		NA
<i>PgB</i>										
Estimate	NA	NA	–1.06	–0.014	1.30	0.027	–2.03	0.008	NA	NA
σ		NA		0.014		0.016		0.05		NA
<i>Pss1</i>										
Estimate	1.10	0.005	2.7	–0.006	–2.01	0.001	–3.02	0.003	0.88	0.021
σ		0.003		0.002		0.002		0.003		0.016
<i>Pws1</i>										
Estimate	–0.66	–0.011	21.36	–0.043	10.29	–0.029	1.15	–0.038	–4.77	0.056
σ		0.008		0.009		0.008		0.018		0.316
<i>Pss2</i>										
Estimate	–1.89	0.023	–1.00	0.035	–2.14	–0.001	–0.18	–0.036	–5.76	0.353
σ		0.022		0.032		0.013		0.024		0.331
<i>Pws2</i>										
Estimate	–0.7	–0.079	–0.42	–0.019	–0.32	–0.019	–1.58	–0.03	–1.07	–0.051
σ		0.117		0.018		0.014		0.029		0.13
<i>Pm3</i>										
Estimate	–3.83	–0.015	0.22	–0.164	0.85	0.212	NA	NA	NA	NA
σ		0.023		0.147		0.304		NA		NA
<i>S</i>										
Estimate	–6.89	–0.001	–10.2	0.011	NA	NA	NA	NA	NA	NA
σ		0.001		0.008		NA		NA		NA
(b)										
<i>Pg1</i>										
Estimate	–1.97	0.002	–1.94	0.001	25.04	–0.013	–2.04	–0.001	–1.92	0.004
σ		0.009		0.003		0.003		0.001		0.007
<i>Pg2</i>										
Estimate	–1.29	–0.02	–0.49	–0.008	–0.15	0.011	–2.05	–0.001	–1.95	–0.036
σ		0.016		0.006		0.008		0.044		0.122
<i>PgB</i>										
Estimate	–2.04	–0.002	–0.49	0.017	–1.35	–0.013	1.33	–0.101	–1.43	0.002
σ		0.029		0.013		0.016		0.069		0.156
<i>Pws0</i>										
Estimate	–1.35	–0.008	3.87	–0.016	4.42	–0.014	–2.45	–0.02	–3.93	0.001
σ		0.015		0.006		0.006		0.011		0.014
<i>Pss1</i>										
Estimate	–1.74	–0.015	–1.24	–0.002	–0.21	–0.005	–2.361	–0.001	–2.73	–0.015
σ		0.014		0.003		0.004		0.005		0.028
<i>Pws1</i>										
Estimate	NA	NA	17.68	–0.056	13.42	–0.068	–1.58	–0.011	NA	NA
σ		NA		0.014		0.02		0.028		NA
<i>Pss2</i>										
Estimate	–2.15	–0.031	–1.93	–0.015	–0.08	0.03	–3.054	0.011	–2.85	–0.021
σ		0.058		0.024		0.029		0.035		0.068

Table 3 (continued)

Component probability*	open		thinned– unburned		thinned–burned		closed		dense	
	ΔAICc	β	ΔAICc	β	ΔAICc	β	ΔAICc	β	ΔAICc	β
<i>Pws2</i>										
Estimate	NA	NA	3.89	−0.048	9.96	−0.048	−2.83	0.032	−3.42	0.004
σ				0.02		0.015		0.073		0.059

Parameter estimates β describe the effect size of a 1-cm increase in annual snowfall on the logit ($\log[P/(1-P)]$) of transition probability P . σ is the standard deviation of the estimate of β . Both parameter estimates come from binomial models in Appendix S3 Eq. 1. ΔAICc values are for the snowpack model minus a null model without the snowpack term. Bold font indicates parameters that were selected for the demographic model. NA values indicate no variance in the probability of interest, so effect of snow could not be modeled.

*Component probabilities are as in Table 2.

weak evidence in support of this growing season mechanism, in the form of a negative effect of snowfall on first-summer survival of Scotch broom (Table 3a). We only found support for this effect in plots that had not been previously burned, however, suggesting that fire may stimulate early springtime germination following snowmelt and thereby allow Scotch broom to overcome otherwise negative effects of snowpack-shortened growing seasons. Interestingly, only Spanish broom was still affected by snowpack during the second winter as a seedling (Table 3b). These strong negative effects of snowpack in combination with the delayed maturity of Spanish broom meant that the demographic model frequently predicted loss of establishing populations prior to reproductive maturity, unless winter snowpack conditions were very low (Fig. 3). This is consistent with expected differences in snowpack tolerance between the species predicted by their invasive and native geographic ranges, namely that Spanish broom is less tolerant of cold winter conditions (Bossard, 2000; Nilsen, 2000).

Because summer soil moisture depletion rates did not differ among treatments, despite large differences in snow depth (e.g. Fig. S1), snowpack depth near the rain–snow transition zone is unlikely to have strong effects on growing season soil moisture, as much of the late winter precipitation in this zone falls as rain once the snow has already melted. If population growth of these species is limited more by growing season duration than by water availability, then low snowpack may paradoxically facilitate drought resistance if higher growth rates during snow-free periods allow the plant to store carbohydrates or increase rooting depth (Franklin, 2013). The cumulative negative effects of snowfall constitute strong evidence that at the rain–snow transition zone in mild montane climates, snowpack can limit populations of evergreen understory plants spreading from lower elevations.

Snowpack and canopy disturbance had complex interactions that varied across species and were not always consistent with our expectations (Fig. 3). For both species, population growth rates were generally lowest in forest stands with dense canopy closure, which were driven by very low germination rates (Table 2), suggesting that low light, low soil temperature, or rapid litter accumulation may suppress germination for both species (Bossard, 1993). Interestingly, the lone snowpack effect in dense canopy was observed at the germination stage of Scotch broom, suggesting that deeper winter snow cover might compound negative effects of shade on Scotch broom germination.

Scotch broom had the highest population growth rate in canopy gaps (Fig. 3a), despite relatively low establishment success, because of rapid maturity and high fecundity of surviving individuals (Table 2). Spanish broom had both reduced establishment and delayed maturity in canopy gaps, resulting in a more modest population growth rate than Scotch broom (Fig. 3b). Low rates of germination and survival in gaps for both species could be due to several factors: First, very young seedlings in springtime are often susceptible to frost heaving of the soil, which can break radicles before they can develop resistance (Goulet, 1995; Castro *et al.*, 2004). We observed evidence of frost heaving at all blocks in canopy gaps, where the planter stakes were often pushed entirely out of the ground. Second, canopy gaps can experience more severe nighttime frosts relative to forest understories, because they lack an insulating canopy layer (Pauli *et al.*, 2013), and thus young seedlings may be killed by repeated frosts. Soil temperature data from a subset of blocks in winter 2013 supported this explanation, as winter soil temperature was consistently lower in gaps than in other canopy classes, and extended soil freezing was only observed in gaps (J.T. Stevens, unpublished data). Third, canopy gaps generally experience greater drought stress than

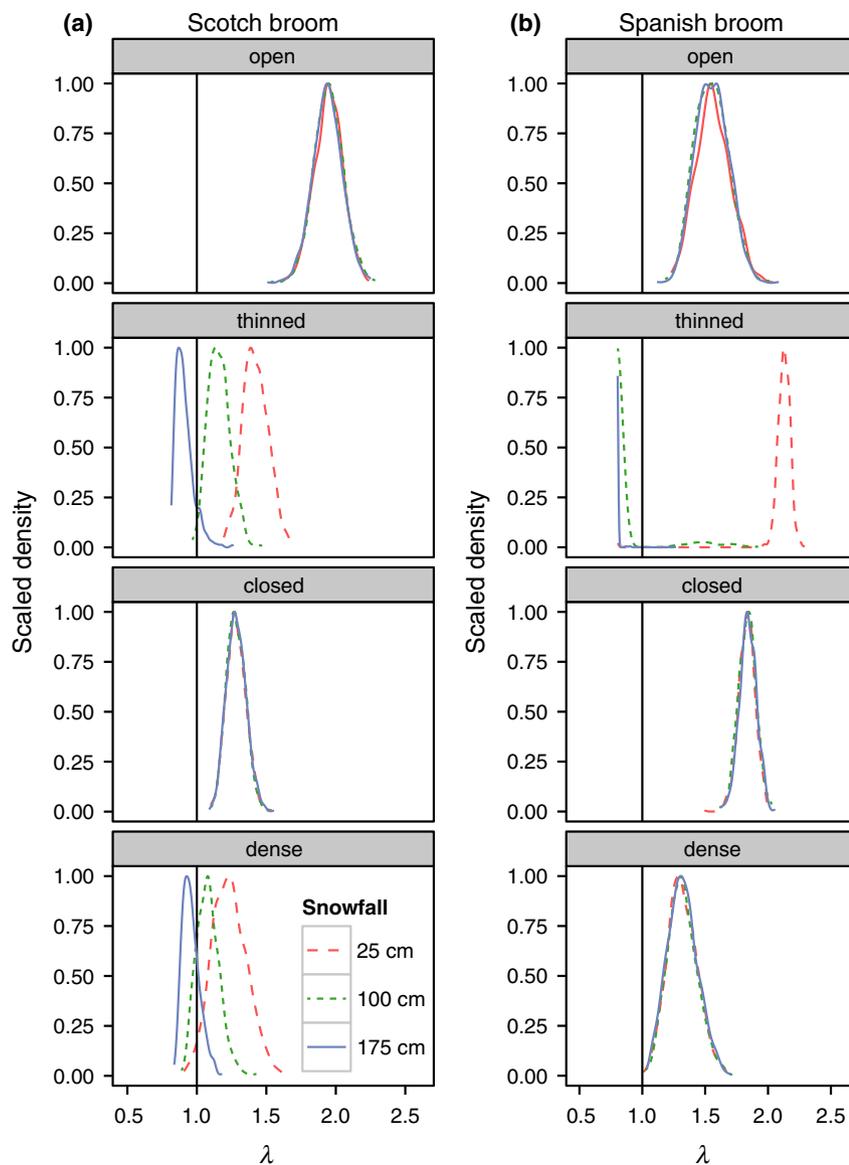


Fig. 3 Density of simulated values of population growth rate (λ) for Scotch broom (a) and Spanish broom (b) under 12 future scenarios representing three annual snowfall totals (red = 25, green = 100, and blue = 175 cm) and four canopy closure conditions (open, thinned, closed, and dense). λ was generated 1000 times for each scenario based on the distribution of modeled parameter estimates assigned by the model selection criteria in Tables 1 and 2. Vertical black line indicates the threshold for positive population growth ($\lambda > 1$).

forest understories, which can contribute to seedling mortality (Mendoza *et al.*, 2009). Summer survival in gaps was also lower for Spanish broom than for Scotch broom (Table 2) – which was unexpected given the higher water use efficiency in Spanish broom – further suggesting that cold winter temperatures may be partially responsible for low establishment success of these species in canopy gaps.

Both broom species exhibited increased initial spring germination in response to fire, which could have been

cued by either heat or smoke (Hanley, 2009; Reyes & Trabaud, 2009). However, we also found that the second-year germination rate of Spanish broom was lower in burned plots than in unburned plots (Table 2b). This is consistent with the finding that high heat of over 100 °C damages Spanish broom seeds but not Scotch broom seeds (Hanley, 2009) and suggests that the Spanish broom seed bank is more at risk of being destroyed by fire than the Scotch broom seed bank. In our demographic models, the negative effects of fire on adult

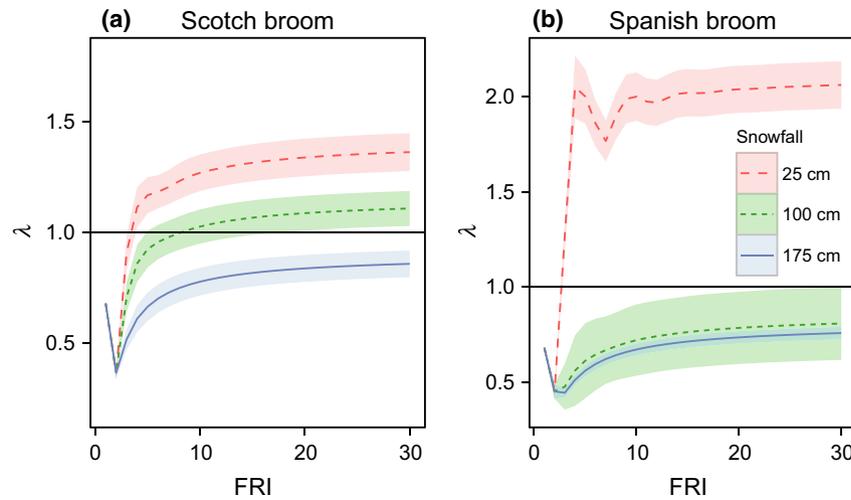


Fig. 4 Simulated values of population growth rate (λ) for Scotch broom (a) and Spanish broom (b) under three future snowfall scenarios (red = 25, green = 100, and blue = 175 cm of annual snowfall), and a range of fire return intervals (FRI) from 0 to 50 years. The shaded region represents ± 1 SD from the mean value of λ at each FRI, based on 1000 iterations of the projection matrix for each scenario. Horizontal black line indicates the threshold for positive population growth ($\lambda > 1$). $\lambda < 1$ for 1 and 2 year FRI's reflect complete mortality of the seedling class.

survival negated the positive effect on germination. While we simulated fall burns after seed dispersal, summer burns that occurred before dispersal would likely compound the negative effects of fire on population growth. Adults of both broom species are usually top-killed by fire, although limited resprouting occurs following low-severity fire (Tveten & Fonda, 1999; Downey, 2000). Therefore, frequent fires may be useful tools for the eradication of broom populations, if a second fire can kill seedlings stimulated by the first fire and thereby further deplete the soil seed bank (Agee, 1996). However, if seedling survival rates are enhanced by reduced snowpack, our data show that fire must be unrealistically frequent (<2 year return interval) under reduced snowpack conditions to prevent rapid population recovery during nonfire years (Fig. 4). In practice, low winter snow cover may act in concert with fire suppression in thinned forest stands to promote invasion by Scotch and Spanish broom to higher elevations.

The scenarios of greatest concern for broom invasion in montane regions have major implications for forest management and plant invasions. If high-emissions forecasts of winter climate change in the Sierra Nevada are accurate, the current rain–snow transition zone may experience complete loss of winter snow cover within 100 years (Maurer, 2007; Cayan *et al.*, 2008). Following over a century of fire suppression in dry mixed-conifer forests on the western slopes of the Sierra Nevada, there are also efforts underway to increase the pace and scale of forest thinning and prescribed fire as fuel treatments, in order to restore forest structure to a more

fire-resilient state (North *et al.*, 2012; Stevens *et al.*, 2014). Therefore, the future forest condition in the rain–snow transition zone of the Sierra Nevada is likely to include more stands with moderate canopy cover and much less snowpack, conditions under which both invasive brooms are predicted to thrive relative to the current dense canopy and moderate snowpack conditions (Fig. 3). While the frequency of fires in the region is also increasing (Westerling *et al.*, 2006; Molotch *et al.*, 2011), it is unlikely that a fire regime with a sufficiently low fire return interval (<3 years) to exclude broom invasion under reduced snowpack scenarios will be either feasible or ecologically desirable from a restoration perspective.

Our data indicate that upslope invasions by lowland plants may be increasingly likely in the future because of relaxed climatic constraints and increased disturbance at higher elevation (Pauchard *et al.*, 2009). While we confirmed that propagule pressure from lowlands is also important (Alexander *et al.*, 2011), we suggest three conditions under which global change might further decrease resistance of montane regions to plant invasions. First, montane invasion risk may be greatest in the rain–snow transition zone, because winter temperatures at these elevations are mild and snow is likely to increase freezing damage. This may be especially likely in Mediterranean regions, where winters are mild and wet. Second, when montane regions are forested, disturbances that reduce canopy cover may have additive effects with climate change to create conditions more suitable for the spread of shade intolerant

lowland invaders. Finally, invasive evergreen shrubs such as brooms may be of particular concern, as they may be more susceptible to freezing by winter snowpack, but also may be well positioned to take advantage of earlier onset growing seasons. Given the particular concern of many land managers over the consequences of invasive shrubs (Mcdougall *et al.*, 2011), we suggest that lowland invasive shrubs should be closely monitored for upslope invasion under global change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Daily fluctuations in nighttime (3:00 am; a) and daytime (3:00 pm; b) soil temperature, and daytime soil volumetric water content (c) from 0 to 5 cm depth from December 2011 through August 2012 (a and b) or November 2012 (c), at a thinned canopy block. Manipulations in February and March 2012 affected the duration of snow cover, as evidenced by both daytime and nighttime temperatures at zero when snow was on the ground, and above zero once snow melted. Manipulations did not directly affect soil moisture (c).

Table S1. Annual mean snowfall totals and associated standard deviation (sd) for each canopy class – snow treatment combination, across the three years of the study. Snow treatment categories are reduced (–), increased (+) and ambient (A).

Table S2. Structure of annual population projection matrix. Annual transition probabilities in this matrix are given in Table 1.

Appendix S3. Statistical models of component probabilities.

Appendix S4. Sensitivity and elasticity scores for Scotch and Spanish broom under different climate-canopy disturbance scenarios.