


Spatiotemporal variation in the strength of density dependence: implications for biocontrol of *Centaurea solstitialis*

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Received: 26 March 2016 / Accepted: 7 June 2017 / Published online: 16 June 2017
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Abstract Invasive plants often occupy large ranges in the introduced region and consequently, local population dynamics vary in ways that affect the potential for biological control. We used matrix models to describe how density and population growth rate of *Centaurea solstitialis* varies in time and space. Matrix models were parameterized with data collected over 4 years from invasions at the coast, interior valleys and Sierra Nevada Mountains in California

(USA). Asymptotic population growth rates (λ) varied dramatically across all populations and years (0.24–6.45), density varied by an order of magnitude and had a measurable effect on survival and λ in all populations. We used simulations to estimate the degree to which a biocontrol agent would need to reduce plant survival to control the weed. Because seedling survival was dependent on density, an agent that reduced seedling density had the effect of increasing the probability that the remaining plants survived to flowering. Interestingly, this meant that in the highest density populations the plant had the largest compensatory response to agent attack and experienced decline ($\lambda \leq 1.0$) only after heavy losses ($\geq 90\%$) to the agent. Conversely, in populations where density was so low that it had only a weak effect on survival, the agent was able to control the plant ($\lambda \leq 1.0$) at much lower levels of attack ($\leq 50\%$). In other words, the impact of a biocontrol agent is predicted to be lower where the plant reaches its highest densities because the surviving plants, now experiencing less intraspecific competition, are more likely to survive to flowering and produce more seeds. This may also be true for other invasive species in which strong density dependent processes are operating. For this reason, prospective agents ought to target density-independence vital rates.

Electronic supplementary material The online version of this article (doi:[10.1007/s10530-017-1476-3](https://doi.org/10.1007/s10530-017-1476-3)) contains supplementary material, which is available to authorized users.

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Keywords Biocontrol · Density dependence · Matrix model

Introduction

Invasion by exotic species is both a cause and a consequence of biotic change worldwide (Vitousek et al. 1997; Wilcove et al. 1998). Invasions themselves are essentially a population-level problem in that density, biomass and the rate at which populations are growing (λ) are measures of invader success (Sakai et al. 2001) and impact (Parker et al. 1999). For the most widespread and well-established invaders, control options are limited. Mechanical and chemical means of control are impractical and/or prohibitively expensive at large spatial scales and may have undesirable impacts on native species and the soil. Biocontrol agents are often seen as the best means of controlling the most widespread invaders (van Driessche et al. 2008). In classical biological control, enemies (typically herbivorous insects) from the invader's native range are released into the introduced range with the expectation that they will suppress the invader's abundance to some ecologically or economically acceptable level. There are a few examples of very successful biocontrol programs including *Senecio jacobaea* in the Pacific Northwest USA (McEvoy and Coombs 1999), *Opuntia ficus-indica* in South Africa (Zimmermann and Moran 1982) and *Hypericum perforatum* in California, USA (Huffaker and Kennett 1959). But the success rate of most biocontrol programs is disappointingly low (McFayden 1998) and there are risks associated with releasing agents, such as host switching (e.g., Arnett and Louda 2002; Rose et al. 2005), interference among agents (e.g., Swope and Parker 2010a), and indirect effects on native insects (Carvalho et al. 2008). It is also difficult to justify the costs associated with testing and releasing agents that would prove to be ineffective.

Demonstrating host-specificity in the agent is key to minimizing the risks associated with host switching, and while this step is essential, it does not address the question of efficacy. Understanding the population behavior of the target weed is the key to releasing agents that will successfully control it, in particular the strength of density dependent survival and fecundity that can suppress population growth (Parker 2000; Ramula and Buckley 2010) and reduce the effectiveness of biocontrol (Garren and Strauss 2009). Unfortunately, biocontrol practitioners rarely have detailed data on the population biology of the weed they are trying to control, much less how population behavior

might vary in time and space. This information would allow them to estimate a prospective agent's likelihood of success prior to deciding whether to release it. Such information would also allow practitioners to decide whether to release an agent across the invaded range or only in some parts of it.

Demographic studies of invasive species are valuable because they can identify whether populations are stable or increasing and at what rate. Measuring the influence of density on survival, growth and reproduction can also identify stages that should not be targeted by control efforts because the plants will be able to compensate for losses (Garren and Strauss 2009). Simulations can estimate the degree to which each vital rate (or combination of rates, as might occur when more than one agent is released) would need to be reduced to achieve control. Collecting the necessary demographic data can be time-consuming, especially given that many invaders occupy large geographic ranges in the introduced range and population behavior is likely to vary considerably over the range, meaning that demographic data may need to be collected from numerous sites. But the increased probability of selecting an agent that effectively controls the weed justifies the time and expense of collecting such demographic data.

For all species, both density and local population dynamics are expected to vary across the geographic range (Hengeveld and Haeck 1982; Brown et al. 1995). This may be especially true for invaders which often occupy large geographic ranges that span numerous environmental gradients that are likely to affect germination, growth, survival and fecundity. In addition to how abiotic factors might affect local population dynamics, variation in the strength of density dependent processes can complicate the influence of biocontrol agents on plant populations. Demographic rates that are strongly dependent on the density of the population can blunt the impact of biocontrol agents. As a hypothetical example, an agent that targets a vital rate with strong density dependence may have the undesirable effect of reducing intraspecific competition and leading to higher survival, growth or fecundity among the surviving plants (Parker 2000; Ramula and Buckley 2010). The strength of density dependence, and thus the interaction between agent attack and invader response, can vary in both time and space (Swope and Parker

2010b). A population persisting under ecologically marginal conditions may never reach densities high enough for it to be a factor, while a population growing under ideal conditions may experience strong density dependence that reduces the impact of the biocontrol agent, meaning that an agent may be least effective where weed density is highest.

Our goal was to describe how density and the population dynamics of established *Centaurea solstitialis* invasions vary across its longitudinal range in California and explore the implications for biocontrol. *C. solstitialis* was introduced to California more than 150 years ago and currently occupies 5.8 million hectares in the state and can be found in 56 of the state's 58 counties (Pitcairn et al. 2006). It has formed persistent invasions in coastal grasslands in the far western part of the state and interior grasslands in the Central Valley. Recently it has begun to invade the mid- and high- elevations of the Sierra Nevada Mountains in the far eastern part of the state. Climatic conditions vary substantially across this range as does *C. solstitialis* density and presumably population dynamics. We wanted to (1) quantify how plant density and population growth rates (λ) vary across the invaded range and through time, (2) use simulation modeling to explore how the strength of density dependent survival affects the ability of a biocontrol agent to control the invasion, and (3) determine whether different populations are likely to respond differently to biocontrol attack due to differences in plant density and the strength of density dependent survival.

Methods

Study species

Centaurea solstitialis L. (yellow starthistle, *Asteraceae*) is native to Eurasia and has an annual lifecycle. Seeds begin to germinate with the onset of autumn precipitation and will germinate throughout the winter so long as there is adequate precipitation. Plants overwinter as rosettes and germination and overwinter survival of rosettes are highly dependent on winter precipitation (DiTomaso and Healy 2007). During the winter the plant invests primarily in taproot growth which it relies on to access deep soil moisture during the summer drought when it flowers (DiTomaso and

Healy 2007). Plants produce inflorescences continuously until the end of their lifecycle in mid- to late-summer. *C. solstitialis* is self-incompatible and depends on generalist insect pollinators, primarily exotic *Apis mellifera* and native *Bombus* species, for reproduction (Sun and Ritland 1998; Benefield et al. 2001; Swope *personal observation*).

The United States Department of Agriculture has introduced six species of pre-dispersal seed predators as biocontrol agents to combat the spread of *C. solstitialis*. Of these, two, the fly *Chaetorellia succinea* (Diptera: Tephritidae; released in 1988) and the weevil *Eustenopus villosus* (Coleoptera: Curculionidae; released in 1990) are common in all five populations in this study (Swope, unpublished data). Another fly, *Urophora sirunaseva* (Diptera: Tephritidae) is rare ($\approx 1\%$ of inflorescences in each population had evidence of attack by this agent). No other biocontrol agents were found in our study populations. Despite their ubiquity statewide, attack by *E. villosus* and *C. succinea* have not satisfactorily controlled *C. solstitialis* invasions in California (DiTomaso and Gerlach 2000, DiTomaso and Healy 2007).

Study sites

Our study sites follow the plant's expansion from coastal areas, across the interior Central Valley to the Sierra Nevada Mountains in the east. Our "coast" site is located in the Loma Alta Open Space Preserve about 20 km from the first vouchered specimen in California (found in 1869). Our "interior" site is located in Mount Diablo State Park where *C. solstitialis* was described as "rare" in 1944 (Ertter and Bowerman 2002) but is now considered the most problematic invasive plant in the Park (Marla Hastings, Mt Diablo State Park, *personal communication*). The "Sierra" site is in the El Dorado National Forest where the plant was first reported in 2000 (Mike Taylor, El Dorado National Forest, retired, *personal communication*).

Study sites differ from one another in characteristics that ought to be important to *C. solstitialis* germination, survival and fecundity, particularly total annual precipitation (ESM Fig. 1). The Coast and Sierra sites receive, on average, the same amount of total precipitation but precipitation is exclusively in the form of rain at the Coast and almost exclusively in the form of snow at the Sierra site. The Interior site has the lowest mean annual precipitation, about half that

of the other two sites, and it also is almost exclusively in the form of rain although snowfall does occasionally occur. Plants at the Sierra site probably experience less drought between precipitation events than plants at the other two sites because the gradual snow melt ought to keep soil moisture levels higher.

In July 2006 we selected two populations at the Coast and Interior sites; one population at each site was on a north-facing slope and the other on a south-facing slope. The north-facing and south-facing populations at the Coast site are ≈ 1.5 km apart; and the north-facing and south-facing populations at the Interior site are ≈ 4 km apart. At the Sierra site, we could not find a population on a north-facing slope so we had only one study population (south-facing slope) at this site. South-facing slopes are anecdotally reported to be where the plant reaches its highest densities and north-facing slopes are considered to be at low risk of invasion (Sheley et al. 1999).

Demographic censusing

We established 15–20 permanent 0.5 m \times 0.5 m plots in each of the five populations, which we will refer to as Coast-N, Coast-S, Interior-N, Interior-S and Sierra-S (the S and N designation refer to the south- and north-facing slopes, respectively). Plots were located randomly throughout each population. If a plot location had landed in an area with no established *C. solstitialis* plants it would have been included in the study so as to describe colonization dynamics; although some plots had very low densities of *C. solstitialis* at the time the study was initiated, none were entirely devoid of the plant. The four corners of each plot were permanently marked with rebar so we could precisely relocate them on each visit. Plants germinate episodically in response to precipitation events and this creates cohorts of plants that can be separated in age by several weeks or even months.

We conducted a census of every plot in each population every 3 weeks beginning after the first rainfall event in the fall and ending 3 weeks after the last rainfall event in the spring. We marked all plants that emerged with a small wooden stake color-coded to identify the germination cohort to which it belonged. We also noted all plants that had died since the last census and the cohort to which each belonged. Plots at the Sierra site were periodically covered by snow and so we were occasionally unable to census

these plots on the scheduled dates so we censused these plots as soon as possible after snowmelt. After the winter rains stopped, we conducted one census to assess survival to flowering and fecundity for every plant. We measured vital rates and λ for four generations (a year runs from October 1st of 1 year to September 30th of the following year; 2006–2007; 2007–2008; 2008–2009; and 2009–2010) in all five populations. We followed the fate of 22,764 seedlings over the 4 years of this study.

When estimating fecundity for each plant, we had to account for larval seed feeding by the biocontrol agents *E. villosus* and *C. succinea*. Both biocontrol agents leave species-specific evidence of having attacked an inflorescence and that made it possible to nondestructively categorize each inflorescence as follows: undamaged by either agent, inflorescences with an *E. villosus* oviposition wound and inflorescences with evidence of *C. succinea* larval feeding. Approximately half of all *E. villosus* eggs or first instar larvae die; in these cases, attacked inflorescences produce as many seeds as unattacked inflorescences (Swope and Parker 2010a). We accounted for this mortality (and the concomitant reduction in seed consumption) in our estimates of seed production in each inflorescence.

We estimated per plant seed production by counting the total number of inflorescences on each plant and categorizing them according to insect attack and multiplying that by the mean number of viable achenes for each of these inflorescence types. Mean number of seed per inflorescence of each attack category was based on lab dissections of 757 inflorescences from the Coast site, 1041 inflorescences from the Interior site and 1590 inflorescences from the Sierra site. Inflorescences for dissection were collected from randomly selected plants outside of our plots.

Very few *C. solstitialis* remain viable in the soil beyond 2 years (Joley et al. 1992; Callihan et al. 1993; DiTomaso et al. 1999) and recruitment from the seed bank appears to be very low relative to current year's seed inputs (Garren and Strauss 2009; Swope and Parker 2010b; Swope and Satterthwaite 2012). We took two approaches to estimating the contribution of the seed bank to recruitment. First, we collected nine soil samples from each population in both June 2007 and June 2008 after germination for that year was over and the adult plants had not yet begun to flower and disperse seed. Soil samples were collected using a

5-cm wide and 15-cm deep soil core from areas between (not in) the plots within the established invasions. We spread each soil sample out in a separate tray in the greenhouse and watered them every 2 days for 5 weeks to see if any *C. solstitialis* seedlings emerged. Seedlings from at least nine other species emerged, but no *C. solstitialis* seedlings did. In another study at the same sites (Swope and Satterthwaite 2012), we tested for a seed bank in the field in the presence of the community of competing plants. We removed the flowering stems of all *C. solstitialis* plants in six 0.5 m × 0.5 m plots in four of our five invasions and counted the number of seedlings that emerged in two successive years (ESM Table 1). The number of seedlings that emerged from the seed bank was in the single digits in the first year and none emerged in the second year. Although some seeds likely survive to germinate in later years, it appears that the seed bank makes a small contribution to recruitment relative to the current year’s seed rain [see also Swope and

Satterthwaite (2012) and Garren and Strauss (2009)] so we did not include a seedbank in the model.

Matrix modeling

We used periodic matrix models to describe the multiple, within year transitions typical of an annual organism (Caswell 2001). Periodic matrix models partition life history transitions into *m* transition periods and each has its own matrix (B_h) that projects into the next period where $h = (1, 2, \dots, m)$. We used an age based classification system to describe *C. solstitialis* life history stages (Fig. 1). Plants that germinate earlier in the year (fall) may be larger and therefore better buffered against periods of unfavorable climatic conditions, resulting in higher survival and fecundity. Plants that germinate late in the year (spring) may still be in the vulnerable seedling stage when the summer drought begins and thus less likely to survive or produce inflorescences. We assigned

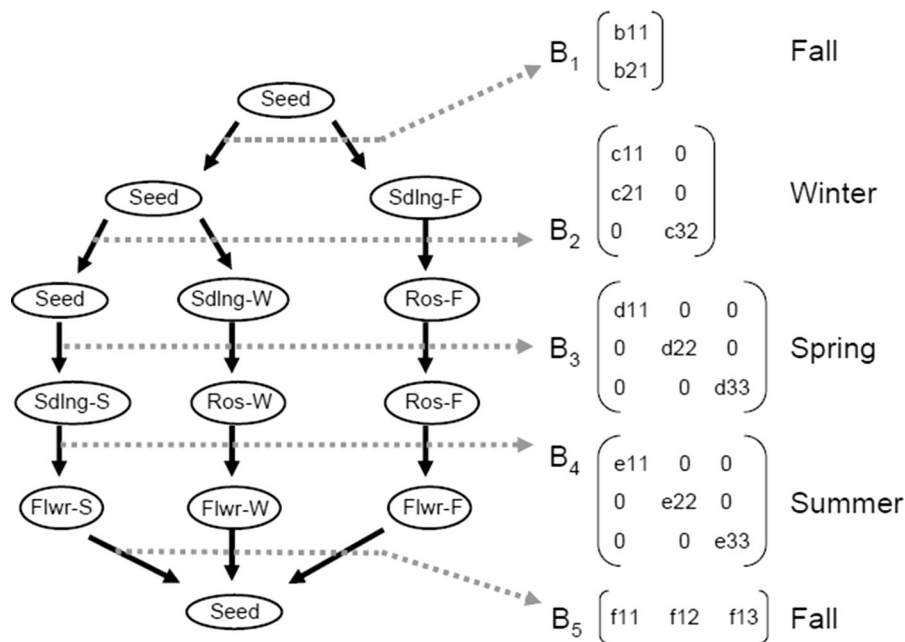


Fig. 1 Life cycle diagram and periodic matrices for *Centaurea solstitialis*. Solid arrows indicate the possible transitions between life stages. Dashed lines indicate which transitions are represented in each matrix (B_h) and the season in which they occurred. B_1 represents the germination (or lack thereof) of seeds in the fall; B_2 represents the germination of the winter cohort seedlings and the survival of the fall cohort seedlings until the winter census; B_3 represents the germination of the

spring cohort seedlings and the survival of both the fall and winter cohort plants until the spring census; B_4 represents the survival of plants in all cohorts to flowering in the summer; B_5 represents fecundities for plants in each cohort. *SdIng* seedling, *Ros* rosette or juvenile plant, *Flwr* flowering plant, the capitalized letters *F*, *W* and *S* following each life stage refers to the season in which the plant germinated (its cohort)

plants to cohorts based on the timing of germination and transitions in the matrices represent survival from one census to the next. Plants that germinated between the first rainfall event (October in each year) and December 31st were assigned to the fall cohort; plants that germinated between January 1st and the last day of February were assigned to the winter cohort; plants that germinated anytime on or after March 1st were assigned to the spring cohort.

Biocontrol simulations

We used the empirically estimated vital rates from the field to parameterize a model in which we simulated the degree to which different levels of attack by a hypothetical biocontrol agent would reduce invader density and λ . In the simulations, we incrementally reduced survival of plants in all cohorts and allowed the simulations to run for 20 time steps (generations for an annual plant) to estimate how the different levels of attack would affect both λ and plant density after two decades of attack.

Statistical analyses

As a general description of how seedling density, flowering plant density and fecundity varied among the five populations and across years, we used general linear models (GLM) in which population and year were the independent variables and $\ln(\text{seedling density})$, $\ln(\text{flowering plant density})$ and $\ln(\text{inflorescences per plant})$ were the dependent variables.

We used logistic regression to describe how cohort, density and population affected the probability that a seedling survived to flowering. We used GLM to test the effect of population, cohort and flowering plant density on the number of inflorescences a plant made. We used inflorescences per plant rather than seeds per plant because attack by the established biocontrol agents reduced seed production. Because density varied dramatically in time and space, we analyzed all years together to get a more accurate picture of its effects across the broadest possible range of densities.

We used MATLAB 7.0 (MathWorks 2011) to empirically estimate asymptotic growth rate (λ), eigenvalues, and eigenvectors. Because we had multiple plots (15–20) for each population, we were able to empirically measure germination, survival and fecundity and calculate λ for each plot and from that,

the mean and its variance for each population in each year.

To determine how density affected a population's growth rate, we plotted empirically estimated growth rates [$\ln(N_{t+1}/N_t)$] against N_t (density the previous year). We then compared the fit of a density independent model, the (linear) Ricker model (Ricker 1954) and the theta logistic negative density dependent models by calculating AIC_c scores and Akaike weights for each. All 4 years of data were analyzed together. We also wanted to determine which factors (population, density and annual precipitation) best predicted population performance. We used GLM with empirically estimated growth rates [$\ln(N_{t+1}/N_t)$] as the response variable and all possible combinations of the independent variables (main effects, main effects with interactions and interactions only). We then calculated the AIC_c scores and Akaike weights to assess the performance of the different models. We calculated the relative importance of population, density and precipitation by summing the Akaike weights for each model containing the factor of interest.

Results

As a plant with an annual lifecycle, *C. solstitialis* is highly responsive to both the total amount of annual precipitation as well as its timing. With one exception (Interior, Year 4), drought dominated at all sites and in all years of this study, with precipitation totals 33–54% of the long-term mean in Year 1; 38–73% of the long-term mean in Year 2; 39–57% of the long-term mean in Year 3; and 42–103% of the long-term mean in Year 4 (ESM Fig. 1).

Spatiotemporal variation in density, survival and fecundity

Across all years of the study, seedling density was lowest in both Coast populations, higher in both Interior populations and highest in the Sierra population (Fig. 2a; Table 1a). In contrast to this consistent spatial pattern in density, there was no clear temporal pattern. For example, the Coast-North population reached its highest average densities in Year 4, while the Sierra-South population had its lowest average density in this same year. The differences in density

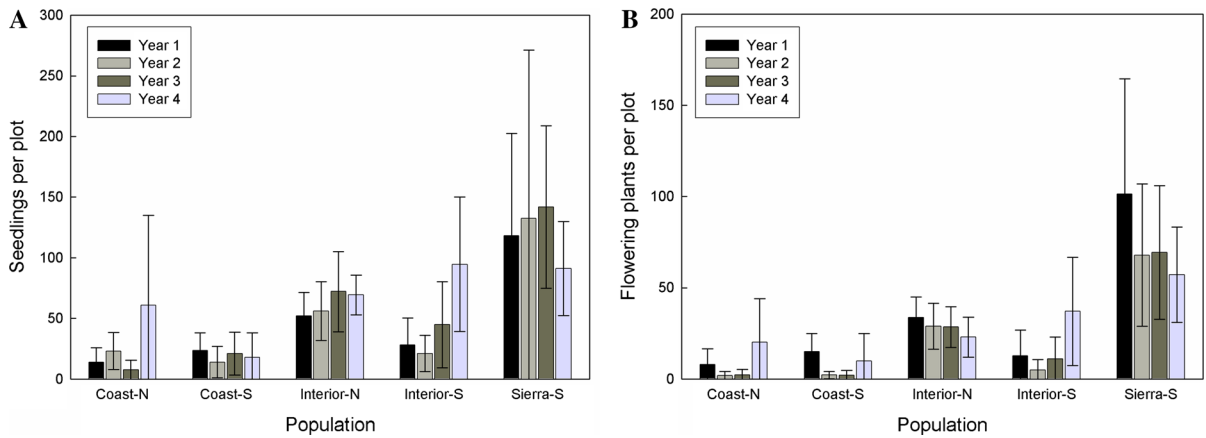


Fig. 2 **a** Mean (± 1 SD) density of *Centaurea solstitialis* seedlings and **b** flowering plants in each population for each year of the study. The letters *N* and *S* following each site refer to the populations on north-facing and south-facing slopes

Table 1 General linear model results for seedling and flowering plant density and fecundity across the five populations in the 4 years of the study

	SS Type III	df	MS	F	<i>p</i>
(A) Seedling density					
Intercept	3961.919	1	3961.919	5937.157	0.0001
Year	9.943	3	3.314	4.967	0.002
Population	185.865	4	46.466	69.632	0.0001
Year \times Population	38.744	12	3.229	4.838	0.0001
Error	210.870	316	0.667		
(B) Flowering plant density					
Intercept	2089.111	1	2089.111	3131.027	0.0001
Year	48.092	3	16.031	24.026	0.0001
Population	342.324	4	85.581	128.263	0.0001
Year \times Population	50.780	12	4.232	6.342	0.0001
Error	210.844	316	0.667		
(C) Inflorescences per plant					
Intercept	2976.072	1	2976.072	5299.729	0.0001
Year	40.869	3	13.623	24.259	0.0001
Population	23.794	4	5.948	10.593	0.0001
Year \times Population	35.820	12	2.985	5.316	0.0001
Error	157.796	281	0.562		

among sites increased as plants progressed to flowering (Fig. 2b; Table 1b). The Sierra plants were, on average, more fecund than plants in any other population (Table 1c). There were no differences in fecundity among the other populations.

In every year \times population combination, a single cohort dominated in terms of abundance but the identity of the dominant cohort varied in time and among populations (ESM Fig. 2). Population, cohort

and local density all affected a plant's probability of surviving to flowering (Table 2). The population to which a plant belonged had a large effect on whether it survived to flowering. Survival was highest in the Sierra-S population (61.8% of seedlings that emerged in the 4 years of the study survived to flowering), followed by the Interior-N (45.9%) and was lowest at the Interior-S and both Coast populations (Interior-S: 34.6%; Coast-N: 30.6%; Coast-S: 36.1%). The cohort

Table 2 Results from logistic regression of seedling survival to flowering as a function of the population and cohort to which a seedling belonged, the year, and density of *C. solstitialis* plants in the plot

	Intercept	SE	Wald χ^2	df	<i>p</i>	Exp(β)	95% CI lower	95% CI upper
Year 1			1067.151	3	0.000			
Year 2	−1.618	0.059	760.606	1	0.000	0.198	0.177	0.222
Year 3	−1.729	0.056	959.882	1	0.000	0.178	0.159	0.198
Year 4	−1.210	0.065	344.900	1	0.000	0.298	0.262	0.339
Pop-CN			628.772	4	0.000			
Pop-CS	0.253	0.092	7.606	1	0.006	1.288	1.076	1.542
Pop-IN	1.162	0.077	230.038	1	0.000	3.195	2.750	3.713
Pop-IS	0.472	0.074	40.784	1	0.000	1.603	1.387	1.853
Pop-SS	1.490	0.072	424.919	1	0.000	4.438	3.852	5.114
Cohort-F			178.551	2	0.000			
Cohort-W	−0.505	0.045	127.269	1	0.000	0.603	0.553	0.659
Cohort-S	−0.671	0.059	131.263	1	0.000	0.511	0.456	0.573
Plant density	−0.004	0.000	324.316	1	0.000	0.996	0.996	0.997
Constant	1.218	0.080	231.386	1	0.000	3.380		

to which a plant belonged was the only variable with a consistent effect on fecundity (fall cohort plants always had the highest fecundity).

Matrix analyses

Across all years of the study, the mean lambda values for each population ranged from 0.24 (Coast-S, Year 2) to 6.45 (Coast-N, Year 3) (Fig. 3). When measured on a per plot basis, λ values ranged from 0.0 (i.e., the *C. solstitialis* population went extinct in that plot) to 40.16. Both Coast populations and the Interior-S population had at least one plot in which *C. solstitialis* went extinct in each year of this 4 year study (with the exception of the Interior-S in Year 4 when no plots experienced local extinction); no plots in the two highest density populations (Interior-N and Sierra-S) ever experienced plot-level extinction of *C. solstitialis*.

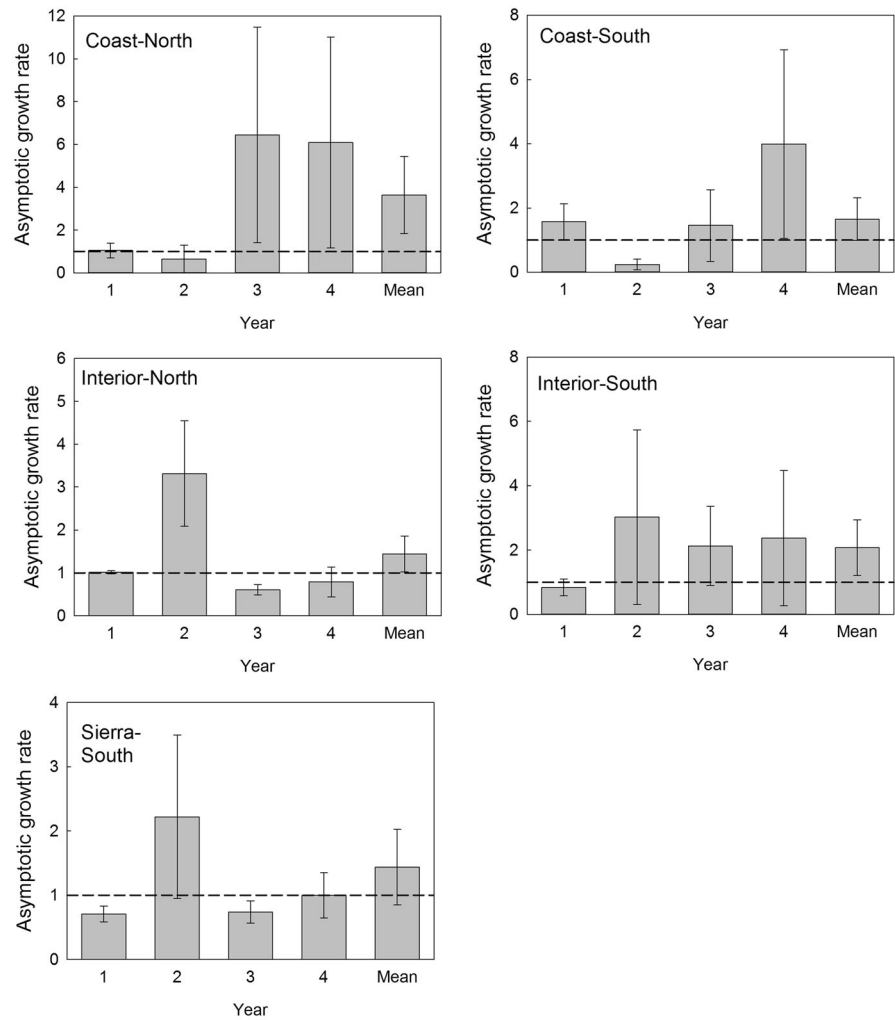
Every population experienced at least 1 year of decline (mean $\lambda < 1.0$) and 1 year of growth (mean $\lambda > 1.0$), sometimes dramatic growth (Fig. 3). Interestingly there was no clear pattern across populations within a single year. For example, in Year 2, a year with below average precipitation at all sites (ESM Fig. 1), the Coast-S population experienced a dramatic decline (mean $\lambda = 0.13$) while the Interior-N

population was growing rapidly (mean $\lambda = 3.31$). Even within a single population, λ values for individual plots varied considerably in the same year, e.g., in Year 4, the Coast-N had one plot in which $\lambda = 40.16$ but another plot that experienced local extinction ($\lambda = 0.0$; ESM Table 2). Despite dramatic variation in λ values across years and the fact that all years experienced below average precipitation, all five populations grew quite rapidly when lambda values were averaged across all years (Fig. 3; ESM Table 2). In some cases, a long-term average $\lambda > 1.0$ was attributable to a single year of rapid growth. The Interior-N population was stable ($\lambda = 1.02$) or declining ($\lambda = 0.61$ and $\lambda = 0.79$) in three of the 4 years but its 4-year average ($\lambda = 1.44$) was due to a single year ($\lambda = 3.31$).

Density and population growth rate (λ)

Our data reveal a negative effect of the population's size on its growth rate in all five of the populations (Fig. 4). At the two Coast populations and the Interior-S, the Ricker function provided the best fit to our data. At the two high density populations (Interior-N and Sierra-S) the theta logistic function was the best fit (Table 3). We compared the resulting r_{adj}^2 values from the best fit models to assess the relative importance of

Fig. 3 Asymptotic growth rate (λ) of each *Centaurea solstitialis* population in the study. Error bars represent 95% C.I.; dashed line at 1.0 represents the point at which a population is neither growing nor declining. The “mean” lambda represents the mean for all 4 years of the study. Note the different scales on the Y axes



population size among the five populations and found that although density had a significant influence on population growth rate at the Coast-N, Coast-S and Interior-S, its influence was rather small in magnitude ($r_{\text{adj}}^2 = 0.13\text{--}0.30$). Density had a larger influence on λ at the Interior-N and the Sierra-S ($r_{\text{adj}}^2 = 0.37$ and 0.59 , respectively).

We evaluated the relative importance of population, density and precipitation on population growth rate by testing all possible combinations of main effects and the interactions among them. The full factorial model was the best fit to the data with an Akaike weight of 0.99, meaning that *C. solstitialis* population behavior cannot be explained without considering all three factors and their interactions. Precipitation had the largest effect on population growth rate. In this model, the effect of density

depended on its interaction with precipitation and population. Because the full factorial model has such a high Akaike weight (0.99), summing the Akaike weights for other models yielded nothing informative.

Biocontrol simulations

We used biocontrol simulations to project the level of damage an agent would need to inflict to reduce either plant density or its population growth rate. We report results from the simulations from three of the five populations, the Coast-N, Interior-N and Sierra-S. Simulations from the low density Coast-N population, where density accounted for relatively little of the variation in λ , showed that this population was the most sensitive to biocontrol attack. Here, any amount of reduction in seedling

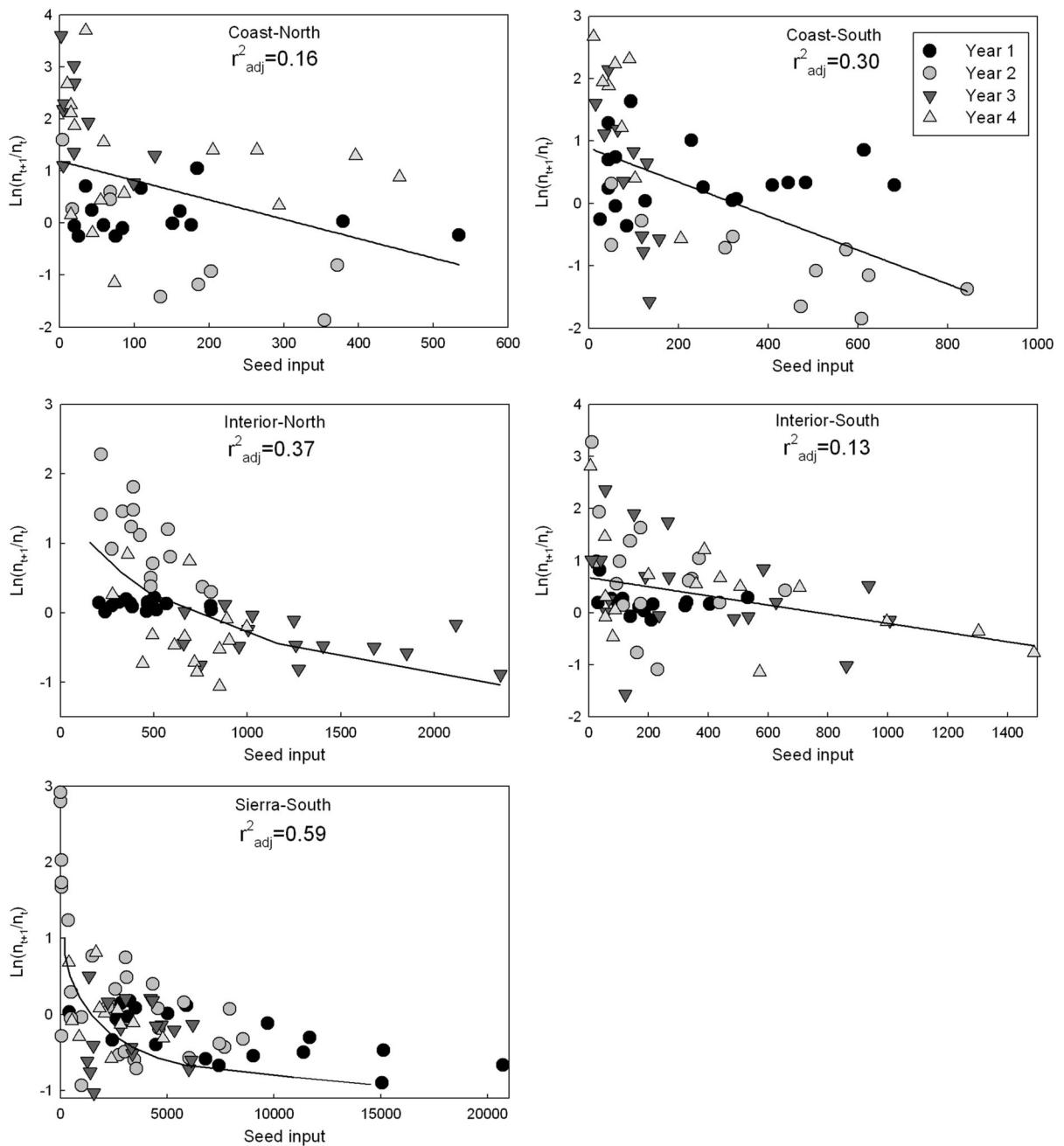


Fig. 4 The effect of *C. solstitialis* population size on its growth rate at the five study populations. The linear Ricker function [$\log(N_{t+1}/N_t) = r(1-N/K)$] was the best fit to the data in both Coast populations and the Interior-S; the theta logistic function [$\log(N_{t+1}/N_t) = r(1-N/K)^\theta$] was the best fit to the data in the

survival caused a reduction in both λ and flowering plant density (Fig. 5). A 50% reduction in seedling survival yielded a population with an average λ of 1.106 but the 95% CI overlapped 1.0, indicating

two highest density populations (Interior-N and Sierra-S). Note the different scales, especially on the X axes. See “Methods: Demographic censusing” for details on how seed input was determined. See Table 3 for r , K and θ values

that this level of attack might cause an otherwise growing population to stabilize or decline over time. A 70% reduction in seedling survival yielded a rapidly declining population at this site and

Table 3 Parameter estimates, residual variance, AIC_c scores and Akaike weights for three models fit to data from five *C. solstitialis* populations

Model	r	K	Theta	Residual variance	r _{adj} ²	AIC _c	Akaike weight
<i>Least squares parameters estimates</i>							
<i>Coast-N</i>							
Density-independent	0.651	–	–	94.776	–	178.12	0.039
Ricker	1.137	173.30	–	79.679	0.49	171.715	0.159
Theta logistic	7.361	116.61	0.035	94.283	0.005	182.497	0.004
<i>Coast-S</i>							
Density-independent	0.145	–	–	75.792	–	162.411	0.000
Ricker	0.84	262.527	–	53.022	0.30	147.540	0.973
Theta logistic	14.336	136.703	0.022	58.633	0.226	154.753	0.026
<i>Interior-N</i>							
Density-independent	0.018	–	–	35.33	–	141.393	0.000
Ricker	0.685	733.63	–	24.776	0.30	122.679	0.121
Theta logistic	3.398	544.078	0.207	22.275	0.37	118.705	0.879
<i>Interior-S</i>							
Density-independent	0.343	–	–	58.531	–	181.842	0.02
Ricker	0.688	626.247	–	50.733	0.133	174.748	0.74
Theta logistic	6.172	305.302	0.04	50.737	0.133	177.026	0.24
<i>Sierra-S</i>							
Density-independent	–0.092	–	–	52.929	–	195.270	0.0001
Ricker	0.301	3080.234	–	42.354	0.20	180.048	0.0001
Theta logistic	7.112	1662.466	0.054	21.844	0.59	130.768	0.999

Note that K (carrying capacity) refers to number of seeds per 0.5 × 0.5 m plot

The best fit model for each population based on Akaike weight is in bold type

flowering plant density would be quite low, perhaps low enough that *C. solstitialis* would no longer be considered an ecological problem.

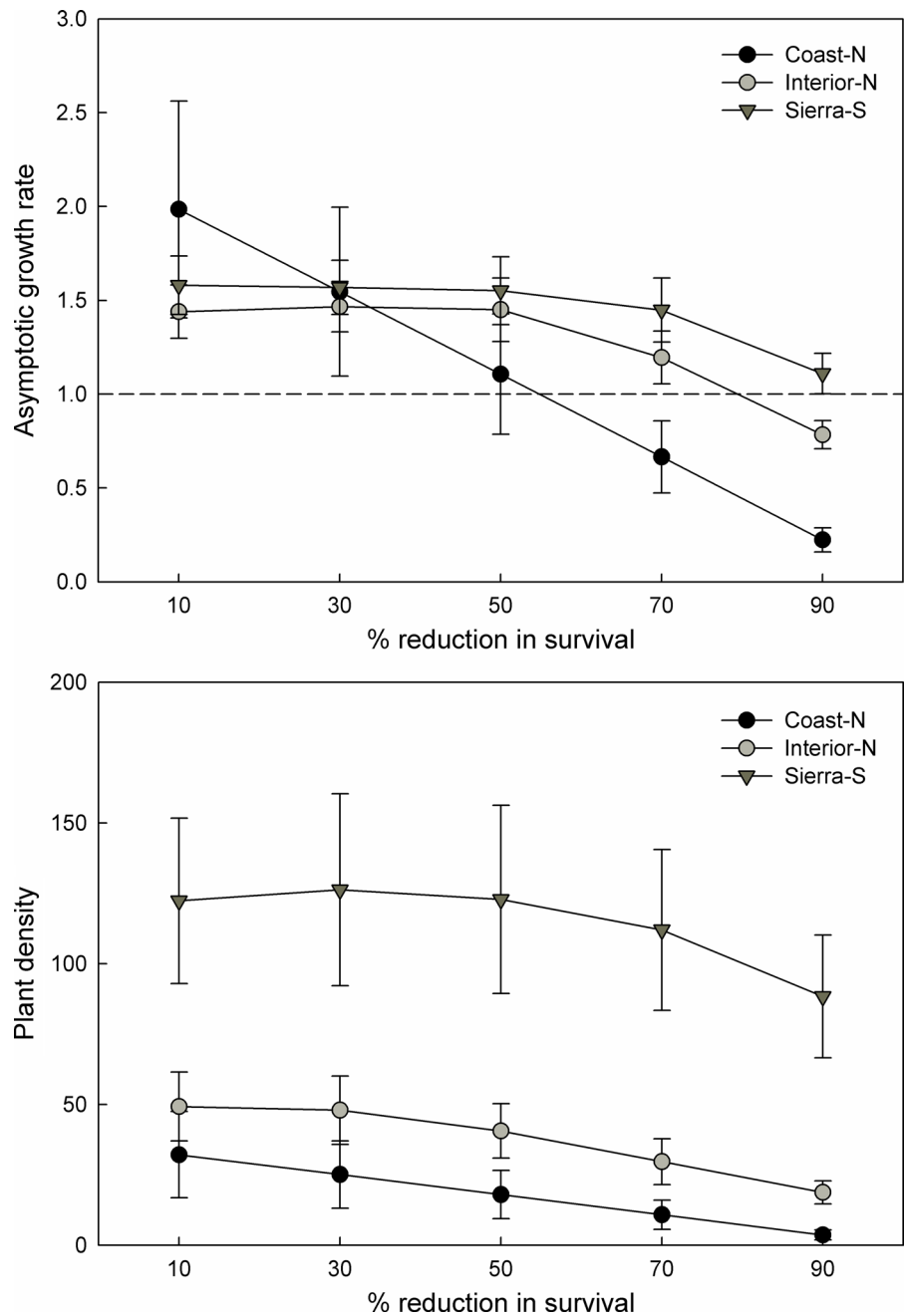
We saw a much different response at the Interior-N and Sierra-S populations where density had intermediate and strong negative effects, respectively, on survival to flowering. At both of these populations, reductions in seedling survival as high as 70% would not cause λ to fall below 1.0. In fact, at the Sierra-S, an agent that reduced seedling survival by 90% would not be sufficient to drive the population to local extinction. Density followed a similar pattern as λ but was somewhat more sensitive to biocontrol attack, meaning that at any given level of simulated biocontrol attack, flowering plant density declined more than did λ , i.e., the population reached a new, lower average equilibrium density but was still persistent or growing. Nevertheless, flowering plant density was still quite

high until attack reduced survival by 70% (Interior-N) or 90% (Sierra-S).

Discussion

Our goals were to describe the abundance and population dynamics of the invasive plant *C. solstitialis* across the invaded range in California, from cool wet coastal areas, to the hot dry interior valleys to the high elevations of the Sierra Nevada Mountains, and explore through simulations how a hypothetical biocontrol agent might affect flowering plant density and λ . Despite dramatic variation in mean λ values for each population across the 4 years of this study, including some years in which populations experienced steep declines, all five populations had a long-term mean $\lambda > 1.0$. *C. solstitialis* density spanned a

Fig. 5 *Upper panel* Asymptotic population growth rates (λ) for three *C. solstitialis* invasions as a function of the percentage of seedlings killed by a hypothetical biological control agent. The *dashed line* at 1.0 indicates a population that is neither growing nor declining. *Lower panel* changes in flowering plant density as a function of the percentage of seedlings killed by a hypothetical biological control agent. We used a mean matrix from all four annual transitions (years 1–4) for these scenarios



range from very low in the coastal populations to very high in the Sierra and density had a measurable effect on survival to flowering and population growth rate in all populations, including the lowest-density ones. Drought also contributed to low population growth rates although there were large swings in λ that appeared to be unrelated to precipitation. The results from our simulation model show that different

populations are likely to respond differently to the same level of biocontrol attack, owing largely to differences in the strength of density-dependence.

Spatial variation in density, survival and fecundity

Our sites differed from one another in terms of temperature, the total amount of precipitation and its

form (rain vs. snow). It has been suggested that *C. solstitialis* is not well-suited to the cool, wet climate typical of coastal California along the western edge of the invasion in the state (DiTomaso and Gerlach 2000; DiTomaso and Healy 2007) and our results are consistent with this observation. *C. solstitialis* density, survival and fecundity were lowest in both Coast populations.

We found that plant density in the Interior-S population was very low and not different from density in either Coast population in the first 3 years of this study. This was surprising given that *C. solstitialis* is perceived to be a greater problem in the interior grasslands than in coastal areas (Pitcairn et al. 2006). It was also surprising that plant density was generally higher on the north-facing slope than on the south-facing slope at the Interior because *C. solstitialis* is anecdotally reported to be most likely to invade south-facing slopes and north-facing slopes are not typically considered to be at high risk of invasion (Sheley et al. 1999).

It has been suggested that the harsh winters in mountainous areas would prevent *C. solstitialis* from invading high elevations (Pitcairn et al. 2002), but our data show that plant density, survival and fecundity were highest in the Sierra population. Elsewhere we have shown that plants at the Sierra are 3.5–4.5 times larger than plants at the Coast and Interior sites (Swope and Parker 2012). The higher densities and survival rates as well as larger size of the Sierra plants indicate that this weed may become as problematic, if not more so, in areas with a montane climate, than it has been elsewhere in the state over the last century and a half.

Density-dependence

Plant density varied by an order of magnitude across sites and years and it had a significant effect on survival to flowering and population growth rate at every site. Density reduced survival in all populations but overall survival rates were highest in the two populations where density was also highest (Interior-N and Sierra-S). Although this may seem counterintuitive, it likely reflects the fact that growing conditions were optimal for the plant at these two sites so the plant reached high densities here and had higher survival rates, even though density-dependent processes were operating. Even the lower density

populations suffered density-dependent mortality, showing that density need not be high for it to have an influence on plant performance.

We used observational plots rather than experimental ones in this study. A limitation of this approach is that it may fail to detect a consistent functional relationship between density and population growth rate. This may be especially true in our study because density naturally ranged from very low (Coast-N = mean 104 seeds per plot, range 4–534) to very high (Sierra-S = mean 4626 seeds per plot, range 376–20,709). Previous work at these same sites (Swope and Parker 2010b) used a combination of experimental and observational plots across a range of seed input levels. Results from the experimental plots showed that plots with the lowest seed inputs had the highest λ values and the plots with the highest seed inputs had the lowest λ values.

We observed considerable small-scale (plot-level) fluctuations in λ , including occasional plot-level extinction or near-extinction as well as plots with $\lambda \gg 1.0$. Plots tended to go extinct in the year after that same plot had very high plant densities; at the same time, plots tended to experience dramatic growth only following a year in which the same plot had very low density (data not shown). Overall, this gives the picture of a single patch experiencing dramatic booms and crashes, while the population as a whole remains relatively stable. One possible explanation for this is interference between last year's dead plants—which remain rooted and upright as skeletons for a year or more—and the new generation of seedlings. High densities of skeletons may reduce seedlings' access to light, thus reducing emergence or survival. This interference would occur only at very fine-spatial scales (e.g., the size of our 0.25 m² plots) and would account for local extinction events as well as exponential growth in the same plot that is independent of site-level factors such as total precipitation and slope aspect. Identifying the mechanism underlying these patch-level booms and busts was outside of the scope of this study, but our data suggest that this is a robust pattern that could be further explored.

Implications for biocontrol

Biocontrol simulations showed that lower levels of attack would be needed to reduce *C. solstitialis* λ and

flowering plant density in the already low-density Coast-N population than would be required in the high-density Interior-N and Sierra-S populations. For example, a 50% reduction in seedling survival at the Coast-N would substantially reduce flowering plant density and may even cause the population to decline ($\lambda \leq 1.0$). But the same level of attack at the Sierra-S site, where plant density is considerably higher, would have no appreciable impact on either flowering plant density or λ . Attack rates in excess of 70% would be required to control the weed at the Interior-N while attack rates of 90% would be necessary to control it in the Sierra, but even then the population would still be growing, albeit more slowly, and flowering plant density would still be higher than at the other sites. The insensitivity of the population growth rate to biocontrol attack at the Interior-N and Sierra-S is driven by strong density-dependent survival such that unattacked plants are more likely to survive as the agent reduces the density of intraspecific competitors. The weak effect of density on survival in the Coast-N population drives this population's linear response to simulated biocontrol attack. This is unfortunate because it means that for any given level of attack, a biocontrol agent will be least effective where plant density is highest (Interior and Sierra) and most effective where plant density is lowest (Coast). However, invader biomass, which we did not measure, is another metric of both invader success and impact and a biocontrol agent that fails to reduce density and/or λ may still reduce biomass.

Centaurea solstitialis is very flexible in the timing of its germination and we found that a different cohort dominated in most year \times population combinations in response to the timing of precipitation. Even though our study was conducted over a 4-year period in which drought dominated, this plant is clearly able to survive under a wide range of climatic conditions that vary in both time and space. Precipitation had the largest effect on λ and future work might experimentally alter water input to assess how this might affect vital rates, λ , the strength of density dependence, and the impact of a biocontrol agent. Hypothetically, water addition might have the effect of increasing seedling survival and thus the strength of density dependence, resulting in an even greater compensatory response in the plant following agent attack. It is also possible that a drought treatment could result in a reduction in both plant survival and the strength of density dependence,

meaning the agent might be more effective in drought years when the plant is already experiencing reduced fitness. Experimental treatments such as this might shed light on how *C. solstitialis* is likely to respond to climate change and whether biocontrol agents may become more or less effective.

Many invasive plants occupy very large geographic ranges in the introduced region, and local population dynamics are likely to vary over such large areas, with implications for biocontrol. Shea et al. (2005) found that the invasive thistle *Carduus nutans* is a short-lived, highly fecund species in New Zealand but a longer-lived, less fecund species in Australia. An agent that destroys seeds is capable of controlling *C. nutans* in New Zealand but not in Australia and a different agent that reduces survival of established plants is capable of controlling the weed in Australia but less so in New Zealand. Similarly, DeWalt (2006) used matrix models to explore the potential of hypothetical biocontrol agents to control *Clidemia hirta* at two sites in Hawaii where it is invasive. One site was an older invasion in closed canopy forest and the other was a more recent invasion in open canopy forest. The invader's abundance and λ were significantly different at two sites. While an agent that destroyed vegetative plants across all size classes was capable of causing population decline ($\lambda < 1.0$), the level of attack required was much higher (64%) at the more recently invaded site and much lower (12%) at the older invasion. Our results are consistent with those of Shea et al. (2005) and DeWalt (2006) in that different populations were differentially susceptible to control by an agent, and this may be generally true for invaders that occupy sites that differ in characteristics that influence local population dynamics.

Ideally, a weed will have one or more vital rates with a large influence on λ and practitioners will be able to find host-specific agents that attack such transitions. Davis et al. (2006) used elasticity analyses to determine that a single agent alone would not control *Alliaria petiolata* even if it attacked one of the two transitions with high elasticities. They also found that two different agents, each one of which attacks a different transition with a high elasticity, would control the target weed. But in some cases, no such demographic Achilles' heel exists. Parker (2000) found that elasticity values were low across all stages of the life cycle of *Cytisus scoparius*, and this may be common in other weed species. In such cases, we can

still use demographic models and simulations to identify the level of attack necessary to control the invader even when the agent attacks a vital rate with little influence on λ . Of course, it may be that the level of attack required would be impossible to achieve in reality (e.g., seed predation rates of 70–99.9% in the highly fecund *C. scoparius*; Parker 2000), but in other cases, it may be possible. Regardless, a demographic approach that incorporates density dependence can estimate the degree to which any one vital rate would need to be reduced to reduce the weed's growth rate and would provide invaluable information to practitioners as they decide which prospective agents to pursue, and which not to pursue.

Strong density dependent processes remain a challenge for biocontrol practitioners. Density dependence suppresses vital rates (survival, growth and fecundity) and consequently λ as well. An agent that attacks a life stage in which density dependence is operating may have the undesirable effect of relaxing the influence of density on survival, growth and fecundity thus increasing the underlying vital rate to produce higher (or even rapid) population growth. Much like the findings here, Garren and Strauss (2009) found that in well-established, high density populations of *C. solstitialis*, agents that reduced fecundity did not reduce plant density because of strong density dependent survival. Ramula and Buckley (2010) showed that targeting a life stage in which density had a strong influence reduced or eliminated the ability of the agent to control the population, but when agents attacked a life stage that occurred after the effects of density had been expressed, the agent had the largest impact on the weed because the plant was unable to compensate. It has been shown here and elsewhere (Garren and Strauss 2009; Swope and Parker 2010b; Swope and Satterthwaite 2012) that density has a strong effect on *C. solstitialis* survival and λ which can reduce or even eliminate the agent's potential to control this plant.

In addition to density and λ , reductions in invader biomass is another measure of biocontrol success. While we measured increased survival to flowering as seedling density decreased, for many species (including *C. solstitialis*) reductions in density may lead to increased biomass among the survivors as well, meaning that biomass per unit area is unchanged or only marginally reduced even as density declines (i.e., constant final yield). In such cases, an agent that reduces plant density would not be considered a

success if the invader's impacts are exerted primarily through biomass.

Plant establishment is often most strongly influenced by the availability of germination microsites rather than seed input (Turnbull et al. 2000) and for this reason, biocontrol attack and interspecific competition may work synergistically to control the invader. When this is the case, a single-species model such as ours will underestimate the degree to which an agent can reduce the target invader. Although our dataset does not allow us to address this possibility directly, we think our single-species model provides a reasonable estimation of the impact (or lack thereof) of seed-feeding biocontrol agents on *C. solstitialis* for two reasons. First, we have experimentally demonstrated widespread seed limited recruitment in this species at these sites (Swope and Parker 2010b), meaning that plant establishment is often not limited by the availability of germination microsites. Secondly, the vital rates and lambdas used here were measured in the context of a diverse and abundant community of competing plants (ESM Table 3). Mean species richness (excluding *C. solstitialis*) per plot ranged from five (Interior-S) to 11 (Coast-N) and, regardless of richness, mean cover was consistently very high, ranging from 72.7% (Interior-S) to 78.5% (Interior-N). Nevertheless, it is true that a reduction in the abundance of an invader (e.g., via biocontrol attack) can lead to secondary invasion by co-occurring exotics or, ideally, recovery by the native species (Pearson et al. 2016), thus working synergistically to reduce invader abundance, and so the potential of a biocontrol agent to control any exotic ought to be considered in a community context.

Concluding thoughts

Many studies investigating the potential of biocontrol agents to control weeds have used λ as the metric of success. We think that in addition to an agent's impact on λ , an agent's impact on density and biomass ought to be used to measure success. The expectation is not necessarily that a biocontrol agent will drive its target to local extinction ($\lambda < 1.0$), but rather that it will reduce its density or biomass to some acceptably low level, although the population may still persist (van Driesche et al. 2008). *Hypericum perforatum* and its agent *Chrysolina quadrigemina* is an often cited example of a highly successful weed-biocontrol system. The agent reduced *H. perforatum* abundance by an order of magnitude and the weed and its agent co-existed in a

stable equilibrium ($\lambda \approx 1.0$) with the agent providing continuous control of the weed for at least a decade after its introduction (Huffaker and Kennett 1959). In this classic example, the measure of the agent's success is not its impact on the weed's λ but rather its impact on its density. Here and elsewhere (Swope and Parker 2010b; Swope and Satterthwaite 2012) we have shown that a single agent can reduce plant density but not cause the population to decline over the longer term.

The strength and form of density dependence poses a challenge for biocontrol practitioners. Our work has also shown that density dependent processes are affected by extrinsic factors such as climate and the competitive community, all of which vary in time and space but nevertheless ought to be explicitly considered when selecting prospective agents as they can reduce the impact of the agent on the invader. Ideally, an agent ought to attack a life stage in which density dependence is not operating so the plant cannot compensate for losses.

Acknowledgements We thank Dan Doak, Carla D'Antonio, Laurel Fox, Kris Hulvey, Alden Griffith and two anonymous reviewers for helpful comments that improved this manuscript. Marci Beitch, Maggie Barr, Aaron Johnson and Joe Braasch ably assisted with the collection of data in the field and the lab. In particular, Joe Braasch deserves thanks for his excellent work counting and categorizing thousands of seeds. SMS is grateful for the support of the Jean Langenheim Fellowship in Plant Ecology and Evolution and an NSF Doctoral Dissertation Improvement Grant DEB-0808337 during the first 2 years of the data collection portion of this study.

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