

# Density dependence, precipitation and biological control agent herbivory influence landscape-scale dynamics of the invasive Eurasian plant *Linaria dalmatica*

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## Summary

1. Resource availability and natural enemies are among the most commonly cited mechanisms affecting competitive ability of invasive plants, but their simultaneous effects on plant dynamics are seldom evaluated in the field. Understanding how endogenous and exogenous factors affect invasive plant abundance is essential when evaluating the impact of classical weed biological control agents because misinterpretations of the mechanisms regulating plant demography may bias inference of herbivore impact.

2. In this study, we report results from a citizen-science monitoring programme initiated to evaluate the effects of the stem-mining weevil *Mecinus janthiniformis* on the Eurasian invasive weed Dalmatian toadflax *Linaria dalmatica*. We used a discrete model of population dynamics to evaluate the relative importance of endogenous and exogenous processes affecting changes in ramet density of *L. dalmatica* at 38 spatially replicated sites in Idaho, USA.

3. Analysis of per-capita population growth rates based on ramet density indicated the presence of direct density dependence, which was most likely due to intraspecific competition. Changes in ramet density were not influenced by the abundance of the resident plant community.

4. Precipitation had a strong, positive effect on ramet density of *L. dalmatica*, while the abundance of *M. janthiniformis* had a weaker, but significant, negative effect after accounting for the density dependence. There was no support for an interactive effect between precipitation and herbivory.

5. *Synthesis and applications.* Our results indicate that biological control is an important factor affecting weed population growth at the landscape scale, but they also suggest that biological control impact may vary considerably on local infestations due to site-specific variation in rainfall and density-dependent processes. We recommend that invasive plant management strategies integrate precipitation and biological control agent monitoring into their programmes to estimate expected biological control efficacy. Alternative control methods should be prioritized in areas where herbivore impact is expected to be low.

**Key-words:** herbivory, invasion ecology, *Linaria*, *Mecinus*, self-regulation, stem-miner, weed population dynamics

## Introduction

Invasive plants have important impacts on agriculture and ecosystem services world-wide (Pysek *et al.* 2011).

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Knowledge of the source, strength and timing of processes that regulate invasive plant populations is integral to their management (Buckley *et al.* 2001; Yokomizo *et al.* 2009). Many invasive plants attain dominance in their recipient communities due to their competitive superiority over native neighbouring species (Levine *et al.* 2003), and one line of evidence suggests that some exotic invasions can be linked to resource availability (Davis, Grime &

Thompson 2000; Walker, Wilson & Lee 2005). Exotic plant species may also gain competitive superiority to native species because they are unaffected by specialist natural enemies ('enemy release hypothesis'; Elton 1958; Keane & Crawley 2002; Mitchell & Power 2003; Blumenthal 2006). Herbivore exclusion studies offer some support for the enemy release hypothesis and more generally, the importance of herbivory on plant population dynamics (Crawley 1989; McEvoy, Cox & Coombs 1991).

While classical biological control is a widely utilized tool in the integrated management of invasive plants, there is poor understanding of how resource conditions, herbivores and other feedback mechanisms simultaneously influence invasive plants. In order to understand why invasive plant abundance fluctuates over time, a better understanding of these processes is needed. Land managers are already faced with the complex task of controlling invasive plants across landscapes with varying biotic conditions and will need to adapt their management strategies to consider alterations in abiotic conditions projected to occur with climate change (IPCC 2007). Projected shifting spatial patterns of precipitation, for example, will have substantial effects on plant community dynamics and their interactions with herbivores. Research that identifies how resource gradients influence regulatory processes affecting invasive plant demography will improve current and future management of invasive plants (Blumenthal 2006).

The invasive weed *Linaria dalmatica* ssp. *dalmatica* (L.) Mill. [syn.: *L. dalmatica* (L.) Mill. and *L. genistifolia* (L.) Mill. ssp. *dalmatica* (L.) Maire & Petitm.] (Plantaginaceae) or Dalmatian toadflax was introduced into North America from Europe near the turn of the 20th century (Alex 1962) and is a noxious weed of natural areas and dry rangelands in 12 western US states and in two Canadian provinces (USDA-NRCS 2013). *Linaria dalmatica* is native to the Dalmatian coast of the former Yugoslavia to Romania, Bulgaria, Albania, Greece, Crete, Turkey, Azerbaijan, Syria, Iran and Iraq (Alex 1962) and has been a target of biological control in North America since the 1960s (Wilson *et al.* 2005). The stem-mining weevil *M. janthinus* Germar was released in North America in the early 1990s because the herbivores previously introduced failed to control *L. dalmatica* (De Clerck-Floate & Harris 2002; Nowierski 2004). Recent morphological and molecular study has found that the stem-mining weevil attacking *L. dalmatica* is actually the newly described cryptic species, *M. janthiniformis* Toševski & Caldara, while *M. janthinus* attacks yellow toadflax, *L. vulgaris* Mill. *Mecinus janthiniformis* is currently established throughout Canada and the western United States (Wilson *et al.* 2005; Toševski *et al.* 2011).

Population abundance of *L. dalmatica* can vary considerably across western North America (Robocker 1970, 1974; Vujnovic & Wein 1997). Ramet density may fluctuate widely in a patch over time, and patches commonly establish, disappear and reestablish within relatively short

time periods (<10 years; Robocker 1974). Clonal growth and seedling recruitment are considered to be important stabilizing processes that compensate for turnover due to the short life span of mature plants (longevity averages 3 years; Robocker 1974). Declines in ramet and patch density in the field have been associated with the release of *M. janthiniformis* (De Clerck-Floate & Miller 2002; Sing *et al.* 2008; Van Hezewijk, Bouchier & De Clerck-Floate 2010), whose adult and larval feeding can reduce shoot height and decrease reproduction of *L. dalmatica* (Schat *et al.* 2011; Goulet *et al.* 2013). One study demonstrated the impact of *M. janthiniformis* to vary with soil N availability (Jamieson *et al.* 2011).

While previous field assessments have shown weevil impact to *L. dalmatica* in the field (De Clerck-Floate & Miller 2002; Sing *et al.* 2008; Van Hezewijk, Bouchier & De Clerck-Floate 2010), they have not explicitly tested how other density-dependent processes (e.g. intraspecific competition) and weather may influence *L. dalmatica* density and top-down regulation by *M. janthiniformis*. Recognition of the simultaneous effects of these processes and how they influence plant regulation by herbivores is critical to improving upon current approaches of invasive plant management using biological control (Shea & Kelly 1998; Buckley *et al.* 2005; Shea *et al.* 2005). For example, analysis of long-term monitoring data of the successful biological control programme against *Salvinia modesta* D. Mitch. in Australia revealed that transitions of *S. modesta* populations between two alternate stable states (e.g. low and high abundance) are driven by stochastic flooding events that affect feedback from weevils (Schooler *et al.* 2011). This example highlights how sensitive invasive plant dynamics can be to their own density and environmental effects on herbivores. This knowledge can be used to improve the predictability and overall efficacy of weed management using biological control.

In this study, we expand upon earlier investigations of *M. janthiniformis* impact on *L. dalmatica* by identifying biotic and abiotic factors that simultaneously influence changes in *L. dalmatica* abundance at the landscape scale. Our main study goals were to determine the factors affecting fluctuations in ramet density of *L. dalmatica* including the effect of *M. janthiniformis* and to assess correlated changes in plant community composition following biological control agent release. Our results indicate that *M. janthiniformis* herbivory impacts interannual changes in *L. dalmatica* density but highlights that other processes strongly affect plant abundance and should be considered when interpreting biological control efficacy.

## Materials and methods

### STUDY SYSTEM

*Linaria dalmatica* is a short-lived, herbaceous perennial that primarily invades well-drained, coarse-textured soils and is commonly

associated with disturbed, sparsely vegetated habitats including roadsides, gravel pits, fields, waste areas, rockslides and other sloped areas (Robocker 1974; Vujnovic & Wein 1997; Blumenthal *et al.* 2012). Seeds can germinate in the fall but more commonly germinate in the spring, and seedling establishment is higher in open areas devoid of competition (Griehop & Nowierski 2002). Individual plants produce multiple prostrate and erect, flowering ramets from mature, woody rootstocks (Vujnovic & Wein 1997). Flowering occurs during mid-summer and extends through late September in most of western North America. Each plant can produce up to 500 000 seeds that can remain viable for up to 10 years. In addition to seed production, *L. dalmatica* also spreads through vegetative horizontal or lateral roots that produce adventitious buds.

*Mecinus janthiniformis* is a univoltine Eurasian weevil that was introduced into Canada in 1991 and the United States in 1995 (De Clerck-Floate & Harris 2002; Nowierski 2004). Adults emerge in early spring, feed on leaves and following ovary maturation begin laying eggs into ramets. Larvae emerge from eggs in approximately 7 days and create mines within the vascular tissue of the ramets (Jeanneret & Schroeder 1992). Pupation occurs during late summer and adults remain in the ramets to overwinter.

#### SITE SELECTION

The Idaho State Department of Agriculture, in partnership with the University of Idaho, Nez Perce Biocontrol Center, U.S. Forest Service and Bureau of Land Management, initiated a statewide effort in 2007 to monitor the changes in *L. dalmatica* and the surrounding plant community following releases of the biocontrol agent *M. janthiniformis*. Populations were selected for

permanent monitoring following a request for potential study sites to land managers and county weed personnel throughout the State of Idaho. The monitoring protocol was developed with the goal to encourage participation of land managers, stakeholders and non-professionals citizen-scientists in the data collection process (see Appendix S1 in Supporting Information). Workshops were conducted annually to train personnel in sampling to improve data quality. Most, but not all, study sites were selected on the basis of accessibility and availability of professional or local participants to monitor sites. We recognize the potential bias of our site selection approach, which was weighed against multiple trade-offs including the logistical constraints of sampling many sites across a wide geographical region within a short time period at locales often in rugged terrain.

Our inquiries lead to the establishment of permanent sampling sites at 17 *L. dalmatica* infestations in 2007, and by 2011, 21 additional sites were added (38 in total). Sites were located within 17 counties (Fig. 1 and Table S1, Supporting Information), nine ecoregions (Level III; McGrath *et al.* 2002) and four land-use classifications (Homer, Fry & Barnes 2012) spanning 2000 m of elevation and seven degrees of latitude (42–49°N). Habitat types of the sites ranged from high-elevation coniferous forests to disturbed areas, river canyon grasslands and pasturelands (see Table S1, Supporting Information).

Since sites were selected for monitoring changes in vegetation following the release of biological control agents, most sites in the study had already received weevil releases in the past (as early as 2000), or weevils were released during the spring in the year that each site was first monitored (see Table S1, Supporting Information). There were only two exceptions (Farragut Water Tower and Porthill) in which no-release records existed. Weevils probably immigrated into these sites during the large

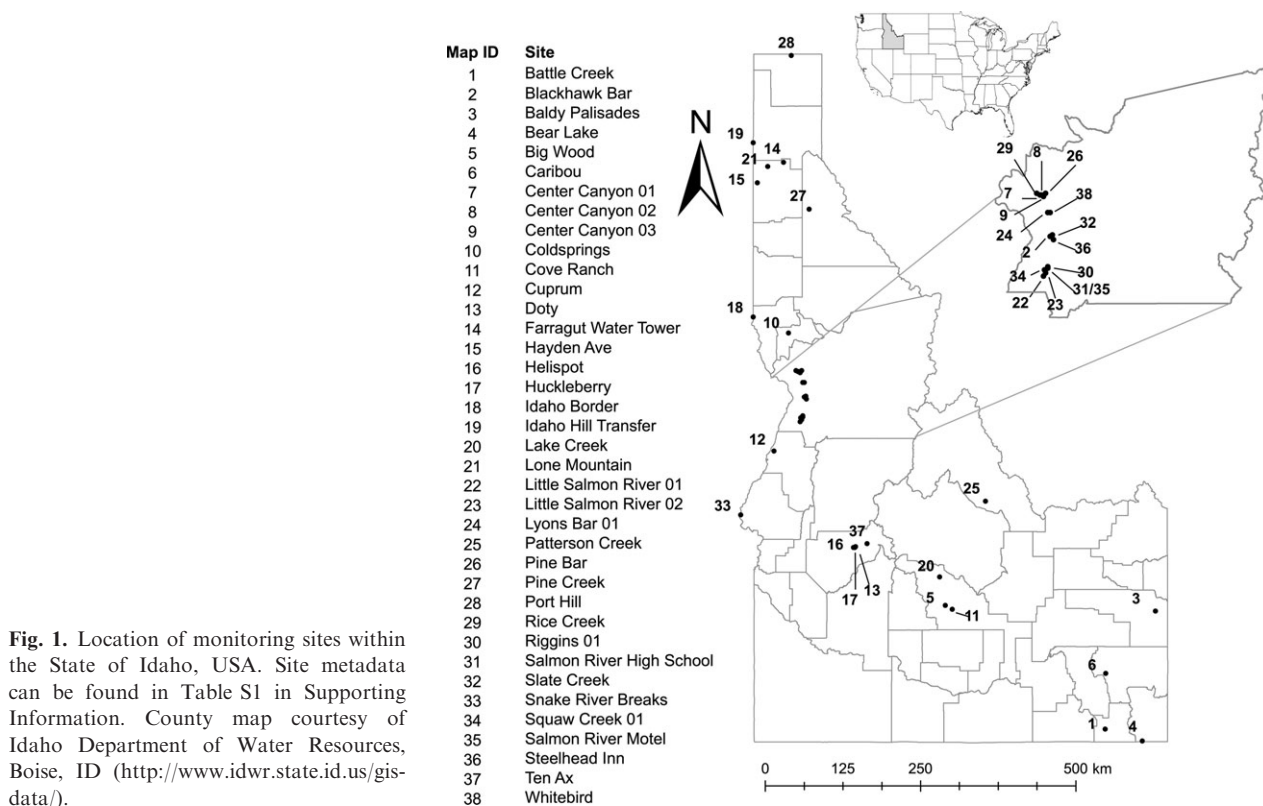


Fig. 1. Location of monitoring sites within the State of Idaho, USA. Site metadata can be found in Table S1 in Supporting Information. County map courtesy of Idaho Department of Water Resources, Boise, ID (<http://www.idwr.state.id.us/gis-data/>).

redistribution programme of *M. janthiniformis* against *L. dalmatica* that began throughout Idaho in the early 2000s. For those sites with known release records, 150–600 weevils ( $221 \pm 17$ , mean  $\pm$  SE) were released per site from 2000 to 2009 (see Table S1, Supporting Information). The recommended release size was 200 weevils but inconsistencies in the number of weevils released per site were usually due to the availability of weevils to individual land managers. Although non-release, control sites would have been the preferred comparison for assessing the impact of *M. janthiniformis*, it was difficult to establish appropriately paired no-release control sites due to weevil prevalence across Idaho and the spatial extent of the effort. However, our approach is valuable for making inference regarding the factors affecting *L. dalmatica* population dynamics due to variation in time since weevil release and variation in abiotic and biotic site conditions.

#### PLANT AND INSECT SAMPLING

Vegetation monitoring was conducted at each site along a permanent 20-m transect placed randomly within a *L. dalmatica* infestation, but generally near the centre of the infested area (see Appendix S1, Supporting Information). Ten permanent  $0.25 \times 0.5$  m ( $0.125\text{-m}^2$ ) sampling plots were marked every 2 m with a stake-whiskered nail along each transect. In each year, the density of erect *L. dalmatica* ramets was counted in each plot. Plant community composition in each plot was characterized in six classes by visually estimating the percentage cover of *L. dalmatica*, native species (perennial grasses and forbs), other exotic invasives (forbs and annual grasses), litter, moss and bare ground. A photograph was taken every year along each transect to visually inspect site-level changes in plant community composition (see Appendix S2, Supporting Information). Monitoring personnel were trained in the identification of common plant species of each broad vegetation cover class. We did not require personnel to identify plants to species level with the exception of *L. dalmatica* because training would have been infeasible, we wanted to avoid misidentifications and were more interested in evaluating general changes in community structure.

The abundance of *M. janthiniformis* was estimated at each site in each year with timed adult counts, which is a fast method for estimating weevil density that is correlated with adult feeding damage and oviposition (Carney 2003). Bluish-black metallic coloured *M. janthiniformis* adults commonly rest near the base of leaves and are conspicuous and easy to count against the pale green colour of *L. dalmatica* leaves and ramets. Six 3-min counts of adults were conducted at each site to estimate weevil abundance. During each count, the observer walked systematically through the entire infestation carefully counting every visible weevil within 3 min.

Vegetation and weevil censuses were conducted on the same day at each site during each year. The monitoring was timed to coincide with peak weevil abundance at each site in that year, which varied greatly across the diverse physiography of Idaho. The most appropriate monitoring times during each year were decided upon based on prior experience with monitoring *M. janthiniformis*, the phenology of *L. dalmatica*, periodic trips to sites to assess weevil activity in any given year and experience of local personnel. Over the entire duration of the study (2007–2011), sites were monitored annually between 22 May and 12 July with

a median monitoring date of 9 June (see Table S1, Supporting Information).

#### CLIMATE DATA

To incorporate measures of climatic variation into our analysis, we queried daily minimum temperature and precipitation data by interpolating values from a 4-km gridded surface (Abatzoglou 2011) for those years that sites were monitored. From these data, we summed precipitation (mm) that fell at a site between 1 May [Julian day (JD): 122] in the year prior ( $t-1$ ) to 30 April (JD: 121) in the next year ( $t$ ). We choose to sum precipitation during this timeframe because all sites were monitored from mid-May until mid-July (Table 1) and we expected plant growth in each year to be most strongly affected by precipitation that fell between monitoring dates. From the temperature data, we extracted the minimum temperature at each site in the winter prior to monitoring ( $T_{min}$ ) because there was an expectation that cold winters may adversely affect *L. dalmatica* and survival of the biological control agent (De Clerck-Floate & Miller 2002).

#### DATA ANALYSIS

Site-level, rather than quadrat-level, estimates of abundance were used in the analysis because weevils were only sampled at the site level and one objective of the analysis was to evaluate the association of weevil abundance to changes in *L. dalmatica* ramet density (see below). We summarized monitoring data prior to the analysis per site by calculating the mean values of *L. dalmatica* ramet density and vegetation cover class values for each year. Counts of *M. janthiniformis* adults were averaged ( $3 \text{ min}^{-1}$ ) per site and for each year. We evaluated patterns in plant community composition by conducting Pearson correlations on the relative abundance (%) of cover classes over the study period (data normalized using standard procedures).

Weed population dynamics are influenced by the simultaneous influence of feedback structure, limiting factors and stochastic processes (Gonzalez-Andujar & Hughes 2000; Lima, Navarrete & González-Andujar 2012). We used a discrete model of population dynamics (Royama 1992; Turchin & Taylor 1992) as the baseline for developing and comparing competing models to understand how these factors explain interannual variation in *L. dalmatica* ramet density. The interannual rate of ramet density change ( $R_t$ ) was calculated as  $R_t = \ln(\text{Stems}_{i+1}) - \ln(\text{Stems}_{it})$ , where  $\text{Stems}_{it}$

**Table 1.** Correlations between vegetation cover classes over the study period

	Pearson correlation coefficients			
	<i>Linaria dalmatica</i>	Bare ground	Perennial grass	Exotic weeds
<i>Linaria dalmatica</i>				
Bare ground	0.14			
Perennial grass	0.07	−0.04		
Exotic weeds	0.13	−0.19*	−0.37***	
Native forbs	−0.03	0.19*	−0.04	−0.29**

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

was the average *L. dalmatica* ramet density ( $0.125 \text{ m}^{-2}$ ) at site  $i$  in current year  $t$  and  $\text{Stems}_{t+1}$  the average density in the following year. We hypothesized that there would be negative feedback (density dependence) on ramet density either in the current ( $t$ ) or in lagged ( $t-1$ ) year denoted by the model  $R_t = \text{Stems}_t + \text{Stems}_{t-1} + \epsilon_t$  (eqn 1), with  $\epsilon_t$  representing sampling error in density estimates plus exogenous (density-independent) effects on *L. dalmatica* population dynamics (Berryman 2003). We used an information theoretic approach to evaluate alternative competing models involving endogenous feedbacks ( $\text{Stems}_t$  and  $\text{Stems}_{t-1}$ ) and exogenous variables thought to affect interannual fluctuations in *L. dalmatica* ramet density (Gonzalez-Andujar & Hughes 2000; Lima, Navarrete & González-Andujar 2012). The potential effects of current and lagged year *M. janthiniformis* adult abundance ( $\text{Mecinus}_t$  and  $\text{Mecinus}_{t-1}$ ) and relative abundance of the individual plant cover classes (*Bare ground*, *Perennial Grasses*, *Forbs* and *Exotic Weeds*) and precipitation (*Precipitation*) and minimum winter temperature (*Tmin*) were evaluated for their contributions as exogenous effects ( $\epsilon_t$ ) on interannual changes in ramet density.

All variables described above and their two-way interactions were included within the initial global model (eqn 1). A linear mixed-effects model using maximum-likelihood estimation was used to estimate model parameters with site included as a random effect using the 'lme4' package in R statistical software version 2.11.1 (R Development Core Team 2010). Preliminary screening indicated that the current year variables ( $t$ ) offered the most explanatory power to those from the lagged year ( $t-1$ ). For example, delayed density dependence ( $\text{Stems}_{t-1}$ ), which might imply an effect of lagged numerical responses by the weevil (Turchin & Taylor 1992; Bonsall, van der Meijden & Crawley 2003), was never important in explaining interannual changes in ramet density. All models found support for the presence of direct density dependence ( $\text{Stems}_t$ ) as found for other weeds (Gonzalez-Andujar & Hughes 2000; Lima, Navarrete & González-Andujar 2012). Time since weevil release was also included into the original model as another test of whether plant dynamics were affected by lags in weevil abundance, but this variable was not important and later dropped from the global model. We also dropped other variables with little or no explanatory power during variable screening as well (e.g. *Forb* cover). Our final model selection approach compared the fit of all the possible candidate models nested within the following global model:

$$R_t = \text{Stems}_t + \text{Mecinus}_t + \text{Perennial Grass}_t + \text{Bare ground}_t \\ + \text{Exotic Weeds}_t + \text{Precipitation}_t + \text{Tmin}_t \\ + \text{their two-way interactions}$$

The fit of each model in the set was then evaluated using second-order Akaike's information criterion (AICc) with the best fit indicated by the lowest AICc. In this approach, each model is ranked using its difference in AICc score with the best-fitting model; models are considered plausible if they have a  $\Delta\text{AICc}$  below 2. The model weight ( $w_i$  = relative likelihood of a model [ $\exp(-0.5 \cdot \Delta\text{AICc}_i)$ ] divided by the sum of likelihoods of all models) was also computed as evidence in support of each model being the best within the set. The relative importance of each predictor was determined by summing the  $w_i$  values across all of the models in the set ( $\sum w_i$ ) in which each predictor occurred (Burnham & Anderson 2002). The multimodel inference analyses were performed using the 'MUMIN' package in R version 2.11.1.

## Results

### TRENDS IN *LINARIA DALMATICA* AND *MECINUS JANTHINIFORMIS* ABUNDANCE

Sites where weevil releases had been conducted between 2000 and 2009 were monitored between 2007 and 2011 to assess plant and weevil abundance (see Table S1, Supporting Information). Variation in the year of weevil release among sites allowed us to summarize general trends across the entire study area over a period of 11 years following weevil releases (Fig. 2). At the landscape scale, ramet density decreased by about 24% during the first 4 years (Fig. 2b). Weevil abundance displayed an incremental increase during this same period increasing in abundance (Fig. 2c), but weevil abundance fluctuated much more than *L. dalmatica* density with peaks in abundance occurring every 3–4 years. Sites with resident weevil populations for at least 9 years (Table S1, Supporting Information) tended to have the lowest ramet densities (Fig. 2b). At the site scale, changes in ramet density during the first 4 years after weevil release were highly variable in direction and magnitude (not shown). Ramet density declined at all sites where weevils had been present for >6 years and were monitored for at least three consecutive years ( $n = 5$ ).

There was little variation in the structure of plant communities among sampling years (Fig. 3), perhaps due to the coarse groupings of vegetation classes. *Linaria dalmatica* cover was always a relatively small ( $7.1 \pm 0.3\%$ , mean  $\pm$  SE) component of the local plant community, uncorrelated with any cover class (Table 1) and displayed a general decrease over time following weevil release (71% reduction from 0 to 11 years after weevil release; Fig. 3). Exotic weeds ( $16.9 \pm 0.5\%$ ) and bare ground ( $23.2 \pm 0.6\%$ ) were the most abundant cover classes followed by native forbs ( $11.8 \pm 0.4\%$ ) and perennial grasses ( $7.6 \pm 0.3\%$ ; Fig. 3). Exotic weed cover (e.g. broadleaved species and annual grasses) was significantly and negatively correlated with all cover classes except *L. dalmatica* (Table 1).

### INTERANNUAL CHANGES IN *LINARIA DALMATICA* RAMET DENSITY

The multimodel inference indicated that interannual changes in *L. dalmatica* ramet density were influenced by negative feedback (endogenous) and exogenous variables (Table 2). Every model indicated the presence of strong, direct density dependence ( $\text{Stems}_t$ ; Fig. 4a). After removing the density-dependent effect, precipitation (*ppt*) and the abundance of *M. janthiniformis* (*Mecinus*) explained further changes in ramet density, but with opposing effects that were consistent among the most plausible models ( $\Delta\text{AICc} < 2$ ; Fig. 4 and Table 2). Changes in ramet density were positively correlated with precipitation (Fig. 4b). On average, ramet abundance increased

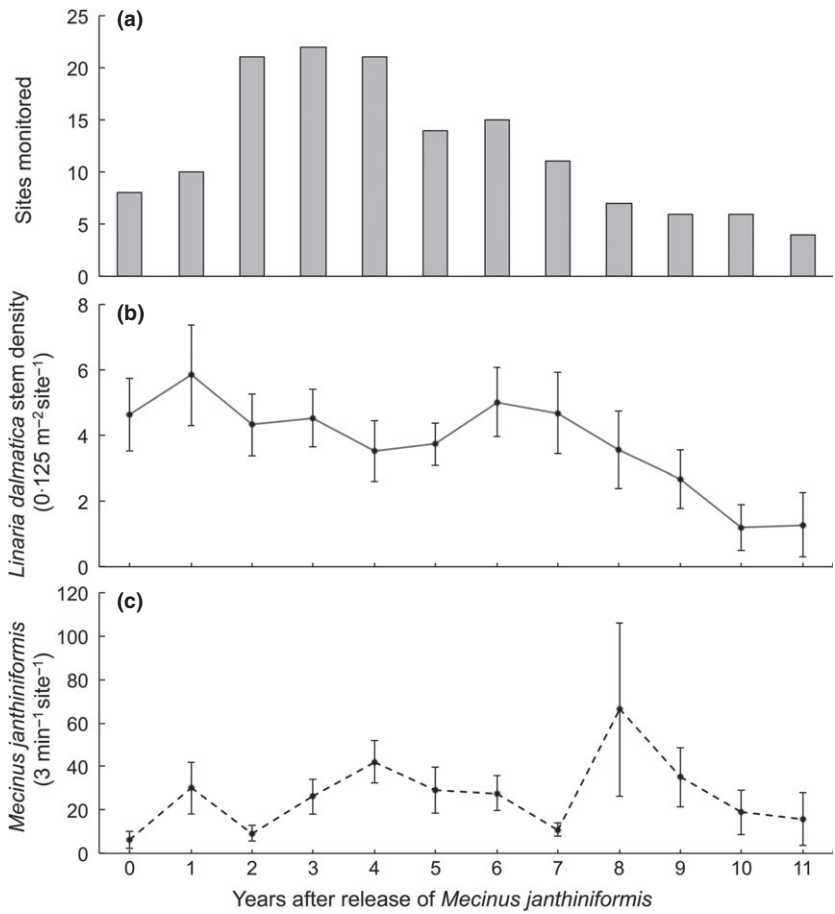


Fig. 2. The number of sites (a) monitored from 2007 to 2011 and sampled abundance of (b) *Linaria dalmatica* ramets and (c) *Mecinus janthiniformis* as a function of weevil release year. Error bars are mean values  $\pm$  1SE.

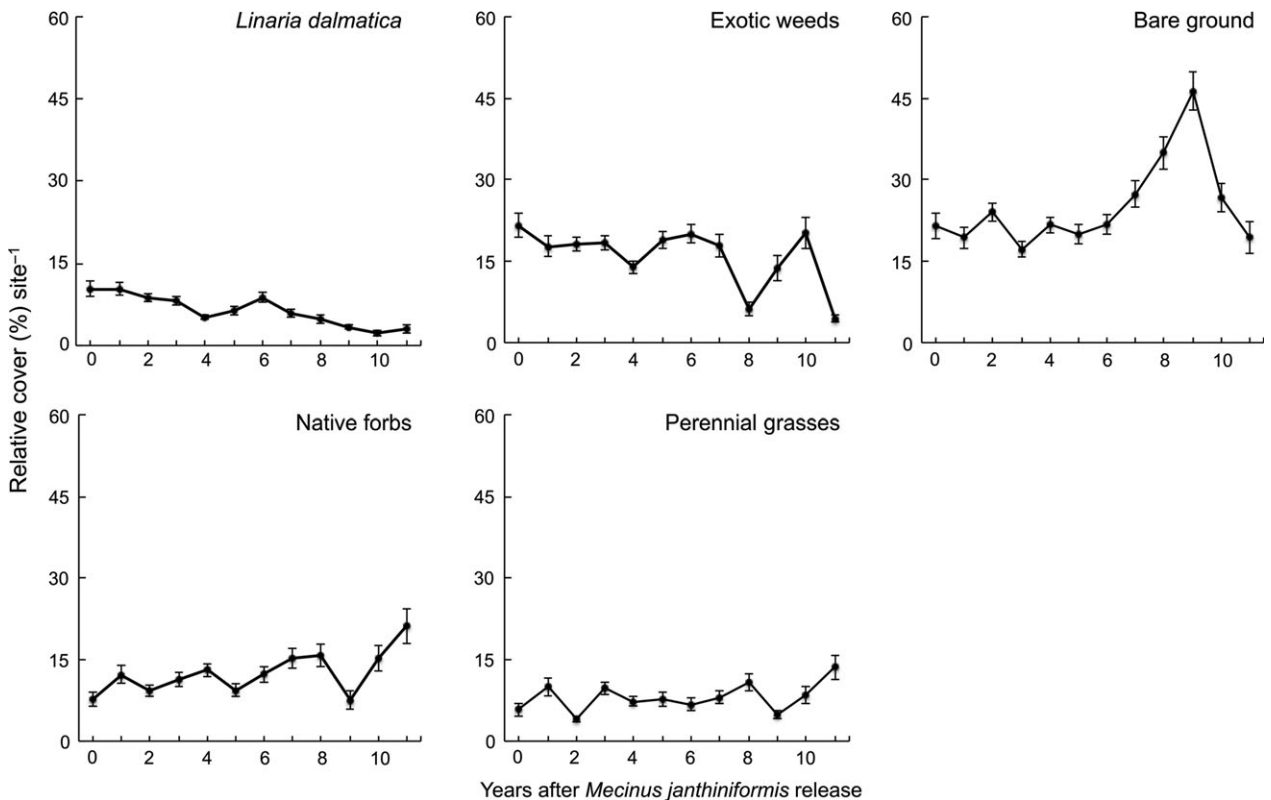


Fig. 3. Changes in plant community composition following release of *Mecinus janthiniformis*. Error bars are mean values  $\pm$  1SE.

**Table 2.** Plausible models ( $\Delta\text{AICc} < 2$ ) explaining interannual changes in ramet density of *Linaria dalmatica* over the period 2007 to 2011. Shown are regression coefficients estimated using maximum likelihood

Model rank	1	2	3	4	5	6	7	8	9	10
$\Delta\text{AICc}$	0	0.35	0.73	0.85	1.32	1.39	1.46	1.5	1.67	1.93
Model weight ( $w_i$ )	0.16	0.13	0.11	0.1	0.08	0.08	0.08	0.07	0.07	0.06
$\Sigma w_i$										
– Intercept	0.142	0.175	0.198	0.251	–0.278	0.162	–0.021	0.190	0.139	–0.061
1.00 Stems <sub>t</sub>	–0.249	–0.246	–0.255	–0.246	–0.252	–0.249	–0.243	–0.245	–0.251	–0.243
0.96 Precipitation ( <i>ppt</i> )	0.001	0.001	0.001	<0.001	0.001	0.001	<0.001	0.001	<0.001	0.001
0.74 Mecinus <sub>t</sub>	–0.034		–0.037	–0.201		–0.042	–0.042	–0.041	–0.188	–0.050
0.47 Perennial grass <sub>t</sub> ( <i>PG</i> )			0.054		0.054	0.067	–0.075		0.044	0.083
0.30 <i>Tmin</i>						0.018		0.013		0.026
0.18 Mecinus <sub>t</sub> * <i>ppt</i>				<0.001					<0.001	
0.14 Bare ground <sub>t</sub>										0.117
0.06 <i>PG</i> * <i>ppt</i>							<0.001			

between years at sites receiving >618 mm of winter precipitation (Fig. 4b). Conversely, weevil abundance (*Mecinus<sub>t</sub>*) had a negative effect on changes in ramet density where, on average, ramet density declined at sites with >9.5 weevils 3 min<sup>–1</sup> (Fig. 4c). There was never strong support among the most plausible models for an interaction between precipitation and weevil abundance (20% of models), which were uncorrelated ( $r = -0.09$ ). Vegetation cover classes were weak contributors to changes in *L. dalmatica* ramet density although *Perennial Grass* appeared in 60% of the top 10 plausible models (Table 2).

## Discussion

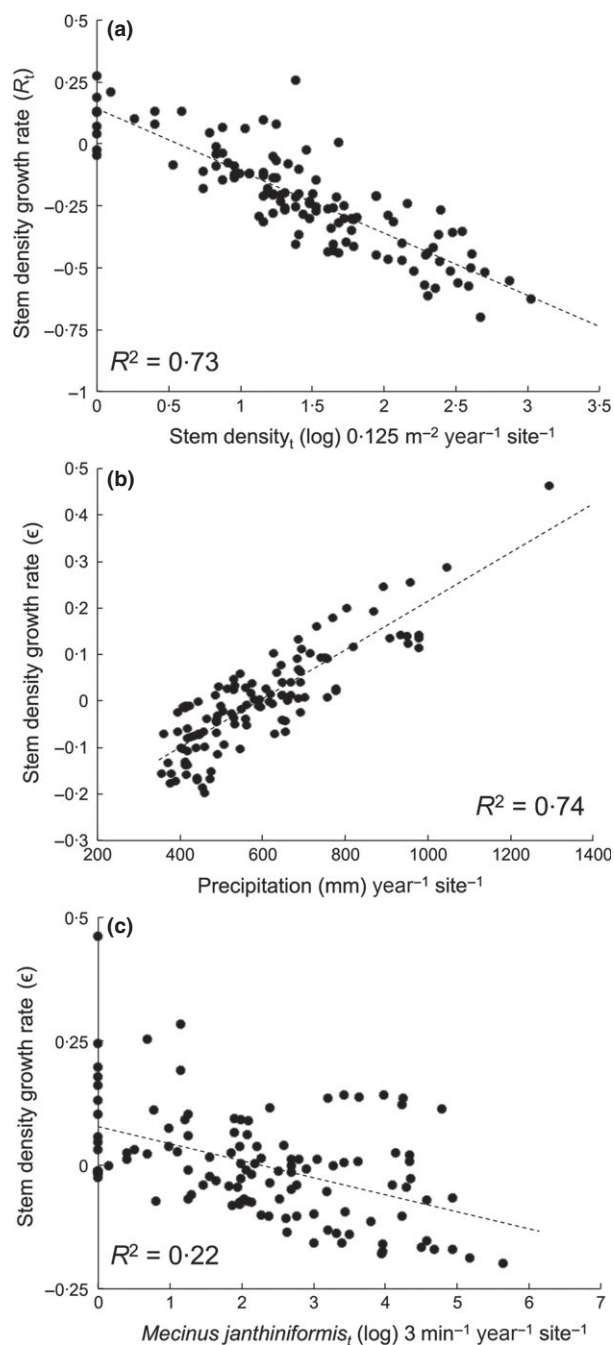
Our model selection approach determined that changes in ramet density of *L. dalmatica* at the landscape scale are affected by direct density dependence, precipitation and the abundance of the biological control agent *M. janthini-formis*. We found little support that *L. dalmatica* dynamics were affected by the abundance of the resident plant community; no vegetation cover classes were correlated with *L. dalmatica* cover or changes in ramet density. This was unexpected given that perennial grass cover influences dynamics of *L. dalmatica* in Washington USA (Robocker 1974) and because plant community composition has been demonstrated to influence *L. dalmatica* dominance (Maron & Marler 2008a,b).

Density-dependent processes are important forces in the population dynamics of organisms with the most common source of self-regulation in plants occurring from competition for resources (Buckley *et al.* 2001; Freckleton & Watkinson 2002; Lima, Navarrete & González-Andujar 2012). In our study, all models strongly supported the presence of direct negative feedback on *L. dalmatica* in Idaho. It is possible that resource competition plays a role in regulating *L. dalmatica* ramet density (Robocker 1974), either through direct competition for nutrients or for light (Freckleton, Watkinson & Rees 2009). For example, as ramet density of the perennial plant *Oclemena acuminatus*

increases, resource availability per ramet decreases, causing a decline in population abundance (Winn & Pitelka 1981).

Interannual changes in ramet density of *L. dalmatica* were also strongly influenced by variation in precipitation, suggesting that rainfall monitoring should be integrated into management practices for predicting population changes. *Linaria dalmatica* ramet density should likely be sensitive to precipitation because water limits growth directly and wet periods cause an increase in available nutrients (Hooper & Johnson 1999; Blumenthal 2009), which stimulates *L. dalmatica* ramet production (Blumenthal *et al.* 2008; Blumenthal 2009). In one study, increased water supply had no effect on the establishment of *L. dalmatica* (Maron & Marler 2008b), but in another study influenced *L. dalmatica* performance and invasion in species-rich communities (Blumenthal *et al.* 2008). Although recruitment was not monitored at our sites, Robocker (1974) suggested that precipitation may also stabilize populations by affecting seedling recruitment which is needed to replace mature plants that commonly live for only 3 years (Robocker 1974).

The abundance of *M. janthini-formis* was the third most important variable contributing to interannual changes in ramet density of *L. dalmatica* across Idaho. Sites with higher weevil abundance were associated with decreasing ramet density. Conversely, sites with fewer weevils were associated with increasing *L. dalmatica* growth rates. Adult and larval feeding has been shown to reduce photosynthesis (Peterson, Sing & Weaver 2005) and may affect plant competitive ability, which may reduce carbohydrate storage and affect plant vigour in the following year (Hunt-Joshi, Blossey & Root 2004). Previous manipulative studies have demonstrated that adult and larval feeding negatively affects the performance of *L. dalmatica* in a single year in a density-dependent manner (Jeanneret & Schroeder 1992; Jamieson *et al.* 2011; Schat *et al.* 2011; Goulet *et al.* 2013) and regional declines in ramet patch density, cover and ramet height have been credited to the release of *M. janthini-formis* (De Clerck-Floate & Miller



**Fig. 4.** Relationship between (a) current year ramet density and interannual changes in *Linaria dalmatica* ramet density (growth rates; i.e. direct density dependence). Relationship between growth rates ( $\epsilon$ ) after removing the density-dependent effect and (b) precipitation and (c) *Mecinus janthiniformis* abundance.

2002; Sing *et al.* 2008; Van Hezewijk, Bouchier & De Clerck-Floate 2010). Important findings from this study are that weevils are having an impact on weed growth rates and counting weevils is a cost-effective method that land managers can use to gauge expected biocontrol impact. It is possible that other introduced herbivores found on *L. dalmatica* [*Brachypterosus pulicarius* (L.), *Calophasia lunula* (Hufnagel), *Eteobalea* spp., and *Rhinusa* spp.] also contribute to changes in weed abundance

(Wilson *et al.* 2005). However, it is assumed that unlike *M. janthiniformis*, these herbivores have a negligible impact on *L. dalmatica* population dynamics because they cause minor damage to *Linaria* growth or reproduction (Grubb, Nowierski & Sheley 2002; Wilson *et al.* 2005).

While this and other studies present evidence suggesting that *M. janthiniformis* negatively affects populations of *L. dalmatica*, it is possible that interannual variation in resource availability may moderate herbivore impact by *M. janthiniformis* to *L. dalmatica* (Wise & Abrahamson 2007). There is some evidence suggesting that resource conditions may interactively affect the impact of *M. janthiniformis*; for example, increases in soil N can diminish plant-level weevil impact (Jamieson *et al.* 2011), while resource limitation and the intensity of weevil attack influence the strength of negative feedback affecting *M. janthiniformis* populations (A.S. Weed, unpublished data) similar to other stem-feeders (Tschardt 1990; Briese, Pettit & Walker 2004). Our model selection procedure, however, indicated that precipitation and herbivory do not interact at the landscape scale – a result also consistent with biological control of spotted knapweed [*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek] in Colorado USA (Maines, Knochel & Seastedt 2013). Other analyses have also revealed that precipitation does not indirectly affect landscape-scale population growth of *M. janthiniformis* (A.S. Weed, unpublished data). These are important findings for the implementation of regional biological control management because herbivory is always having an impact that is independent of the amount of rainfall.

There are still many aspects of *L. dalmatica* population ecology that are not well understood which are needed to adapt weed management practices for optimal efficiency. Further study is needed to understand how stochastic environmental events influence other population (e.g. seed bank dynamics and recruitment) and community-level (e.g. competition) processes so management can then be developed to exploit these demographic effects. In addition, recognition of the spatial scale at which one would expect plant abundance and biological control impact to be similar will also help to prioritize management practices.

Our results lend further support to the notion that management of invasive weeds and evaluations of biological control impact require an understanding of how exogenous and endogenous processes simultaneously affect weed population dynamics. This study and others (Shea *et al.* 2005; Schooler *et al.* 2011) emphasize that the timing and strengths of feedbacks operating on biological systems are likely to be sensitive to resource pulses with outcomes that are consequential to management. For example, weevil impact to *L. dalmatica* is expected to be low at sites receiving relatively large inputs of precipitation. Our study also demonstrates that weevil counting provides a robust method of estimating anticipated impact of biological control. We recommend that land managers monitor winter precipitation and assess weevil abundance on an annual



basis to evaluate whether biological control is a practical long-term control strategy at their sites and to prioritize areas for alternative control methods where weevil impact is expected to be low. Given the strong influence of precipitation on *L. dalmatica* growth rates and other co-occurring noxious weeds (e.g. *Centaurea*; Maines, Knochel & Seastedt 2013), we expect new challenges to emerge for weed managers in dryland ecosystems as new patterns of precipitation are projected with climate change. Results from this study can be used to estimate current and predicted future changes in suitable weed habitats to identify areas where management efforts should focus on reducing propagule pressure to prevent new infestations.

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## Data accessibility

Field sampling data: DRYAD entry doi:10.5061/dryad.2gj70.

## References

- Abatzoglou, J.T. (2011) Development of gridded surface meteorological data for ecological applications and modeling. *International Journal of Climatology*, **33**, 121–131.
- Alex, J. (1962) The taxonomy, history, and distribution of *Linaria dalmatica*. *Canadian Journal of Botany*, **40**, 295–307.
- Berryman, A.A. (2003) On principles, laws and theory in population ecology. *Oikos*, **103**, 695–701.
- Blumenthal, D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, **9**, 887–895.
- Blumenthal, D.M. (2009) Carbon addition interacts with water availability to reduce invasive forb establishment in a semi-arid grassland. *Biological Invasions*, **11**, 1281–1290.
- Blumenthal, D.M., Chimner, R.A., Welker, J.M. & Morgan, J.A. (2008) Increased snow facilitates plant invasion in mixedgrass prairie. *New Phytologist*, **179**, 440–448.
- Blumenthal, D.M., Norton, A.P., Cox, S.E., Hardy, E.M., Liston, G.E., Kennaway, L., Booth, D.T. & Derner, J.D. (2012) *Linaria dalmatica* invades south-facing slopes and less grazed areas in grazing-tolerant mixed-grass prairie. *Biological Invasions*, **14**, 395–404.
- Bonsall, M.B., van der Meijden, E. & Crawley, M.J. (2003) Contrasting dynamics in the same plant–herbivore interaction. *Proceedings of the National Academy of Sciences*, **100**, 14932–14936.
- Briese, D., Pettit, W. & Walker, A. (2004) Evaluation of the biological control agent, *Lixus cardui*, on *Onopordum* thistles: experimental studies on agent demography and impact. *Biological Control*, **31**, 165–171.
- Buckley, Y.M., Hinz, H.L., Matthies, D. & Rees, M. (2001) Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecology Letters*, **4**, 551–558.
- Buckley, Y.M., Rees, M., Sheppard, A. & Smyth, M. (2005) Stable coexistence of an invasive plant and biocontrol agent: a parameterized coupled plant–herbivore model. *Journal of Applied Ecology*, **42**, 70–79.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer Verlag, New York.
- Carney, V.A. (2003) *Ecological interactions of biological control agent, Mecinus janthinus Germar, and its target host, Linaria dalmatica (L.) Mill.* MS thesis, University of Lethbridge.
- Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology*, **34**, 531–562.
- Davis, M., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
- De Clerck-Floate, R. & Harris, P. (2002) *Linaria dalmatica* (L.) Miller, broad-leaved Dalmatian toadflax (Scrophulariaceae). *Biological Control Programmes in Canada 1981–2000* (eds P. Mason & J. Huber), pp. 368–374. CABI Publishing, Wallingford, UK.
- De Clerck-Floate, R. & Miller, V. (2002) Overwintering mortality of and host attack by the stem-boring weevil, *Mecinus janthinus* Germar, on Dalmatian toadflax (*Linaria dalmatica* (L.) Mill.) in western Canada. *Biological Control*, **24**, 65–74.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Freckleton, R.P. & Watkinson, A.R. (2002) Are weed population dynamics chaotic? *Journal of Applied Ecology*, **39**, 699–707.
- Freckleton, R., Watkinson, A. & Rees, M. (2009) Measuring the importance of competition in plant communities. *Journal of Ecology*, **97**, 379–384.
- Gonzalez-Andujar, J.L. & Hughes, G. (2000) Complex dynamics in weed populations. *Functional Ecology*, **14**, 524–526.
- Goulet, E.J., Thaler, J., DiTommaso, A., Schwarzländer, M. & Shields, E.J. (2013) Impact of *Mecinus janthinus* (Coleoptera: Curculionidae) on the growth and reproduction of *Linaria dalmatica* (Scrophulariaceae). *Great Lakes Entomologist*, **46**, 90–98.
- Grieshop, M.J. & Nowierski, R.M. (2002) Selected factors affecting seedling recruitment of Dalmatian toadflax. *Journal of Range Management*, **55**, 612–619.
- Grubb, R., Nowierski, R.M. & Sheley, R. (2002) Effects of *Brachyterolus pulicarius* (L.) (Coleoptera: Nitidulidae) on growth and seed production of Dalmatian toadflax, *Linaria genistifolia* ssp. *dalmatica* (L.) Maire and Petitmengin (Scrophulariaceae). *Biological Control*, **23**, 107–114.
- Homer, C.C., Fry, J.A. & Barnes, C.A. (2012) *The National Land Cover Database, U.S. Geological Survey, Fact Sheet 2012–3020*, 4 pp.
- Hooper, D.U. & Johnson, L. (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry*, **46**, 247–293.
- Hunt-Joshi, T., Blossey, B. & Root, R.B. (2004) Root and leaf herbivory on *Lythrum salicaria*: implications for plant performance and communities. *Ecological Applications*, **14**, 1574–1589.
- Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC*. Cambridge University Press, Cambridge.
- Jamieson, M.A., Knochel, D., Manrique, A. & Seastedt, T.R. (2011) Top-down and bottom-up controls on Dalmatian toadflax (*Linaria dalmatica*) performance along the Colorado Front Range, USA. *Plant Ecology*, **213**, 185–195.
- Jeanneret, P. & Schroeder, D. (1992) Biology and host specificity of *Mecinus janthinus* Germar (Col.: Curculionidae), a candidate for the biological control of yellow and Dalmatian toadflax, *Linaria vulgaris* (L.) Mill. and *Linaria dalmatica* (L.) Mill. (Scrophulariaceae) in North America. *Biocontrol Science and Technology*, **2**, 25–34.
- Keane, R. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164–170.
- Levine, J.M., Vilà, M., Antonio, C.M.D., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 775–781.
- Lima, M., Navarrete, L. & González-Andujar, J.L. (2012) Climate effects and feedback structure determining weed population dynamics in a long-term experiment. *PLoS ONE*, **7**, e30569.
- Maines, A., Knochel, D. & Seastedt, T. (2013) Biological control and precipitation effects on spotted knapweed (*Centaurea stoebe*): empirical and modeling results. *Ecosphere*, **4**, art80.
- Maron, J.L. & Marler, M. (2008a) Effects of native species diversity and resource additions on invader impact. *American Naturalist*, **172**, S18–S33.
- Maron, J.L. & Marler, M. (2008b) Field-based competitive impacts between invaders and natives at varying resource supply. *Journal of Ecology*, **96**, 1187–1197.

- McEvoy, P.B., Cox, C. & Coombs, E.M. (1991) Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecological Applications*, **1**, 430–442.
- McGrath, C.L., Woods, A.J., Omernik, J.M., Bryce, S.A., Edmondson, M., Nesser, J.A. *et al.* (2002) *Ecoregions of Idaho (Color Poster with Map, Descriptive Text, Summary Tables, and Photographs)*. US Geological Survey Map (1: 1,350,000). US Geological Survey, Reston, Virginia.
- Mitchell, C.E. & Power, A.G. (2003) Release of invasive plants from fungal and viral pathogens. *Nature*, **421**, 625–627.
- Nowierski, R.M. (2004) *Mecinus janthinus*. *Biological Control of Invasive Plants in the United States* (eds E.M. Coombs, J.K. Clark, G.L. Piper & A.F. Cofrancesco), pp. 392–394. Oregon State University Press, Corvallis, OR.
- Peterson, R.K.D., Sing, S.E. & Weaver, D.K. (2005) Differential physiological responses of Dalmatian toadflax, *Linaria dalmatica* L. Miller, to injury from two insect biological control agents: implications for decision-making in biological control. *Environmental Entomology*, **34**, 899–905.
- Pysek, P., Jarosik, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. (2011) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725–1737.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robocker, W. (1970) Seed characteristics and seedling emergence of Dalmatian toadflax. *Weed Science*, **18**, 720–725.
- Robocker, W. (1974) Life history, ecology and control of Dalmatian toadflax. *Technical Bulletin of the Washington Agricultural Experiment Station*, **79**, 1–20.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, London, UK.
- Schat, M., Sing, S., Peterson, R. & Menalled, F. (2011) Growth inhibition of Dalmatian toadflax, *Linaria dalmatica* (L.) Miller, in response to herbivory by the biological control agent *Mecinus janthinus* Germar. *Journal of Entomological Science*, **46**, 232–246.
- Schooler, S.S., Salau, B., Julien, M.H. & Ives, A.R. (2011) Alternative stable states explain unpredictable biological control of *Salvinia molesta* in Kakadu. *Nature*, **470**, 86–89.
- Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, **8**, 824–832.
- Shea, K., Kelly, D., Sheppard, A.W. & Woodburn, T. (2005) Context-dependent biological control of an invasive thistle. *Ecology*, **86**, 3174–3181.
- Sing, S., Weaver, D., Nowierski, R.M. & Markin, G.P. (2008). Long-term field evaluation of *Mecinus janthinus* releases against Dalmatian toadflax in Montana (USA). *Proceedings of the XII International Symposium on Biological Control of Weeds, La Grande Motte, France, 22–27 April, 2007* (eds M.H. Julien, R. Sforza, M.C. Bon, H.C. Evans, P.E. Hatcher, H.L. Hinz & B.G. Rector), pp. 620–624. CABI Publishing, Wallingford, UK.
- Toševski, I., Caldara, R., Jović, J., Hernández-Vera, G., Baviera, C., Gassmann, A. & Emerson, B.C. (2011) Morphological, molecular and biological evidence reveal two cryptic species in *Mecinus janthinus* Germar (Coleoptera, Curculionidae), a successful biological control agent of Dalmatian toadflax, *Linaria dalmatica* (Lamiales, Plantaginaceae). *Systematic Entomology*, **36**, 741–753.
- Tscharntke, T. (1990) Fluctuations in abundance of a stem-boring moth damaging shoots of *Phragmites australis*: causes and effects of overexploitation of food in a late-successional grass monoculture. *Journal of Applied Ecology*, **27**, 679–692.
- Turchin, P. & Taylor, A.D. (1992) Complex dynamics in ecological time series. *Ecology*, **73**, 289–305.
- USDA-NRCS (2013) *The PLANTS Database*. National Plant Data Center, Baton Rouge, LA 70874-4490, USA. Available at <http://plants.usda.gov> (accessed 15 March 2013).
- Van Hezewijk, B.H., Bourchier, R. & De Clerck-Floate, R. (2010) Regional-scale impact of the weed biocontrol agent *Mecinus janthinus* on Dalmatian toadflax (*Linaria dalmatica*). *Biological Control*, **55**, 197–202.
- Vujnovic, K. & Wein, R.W. (1997) The biology of Canadian weeds. 106. *Linaria dalmatica* (L.) Mill. *Canadian Journal of Plant Science*, **77**, 483–491.
- Walker, S., Wilson, J.B. & Lee, W.G. (2005) Does fluctuating resource availability increase invasibility? Evidence from field experiments in New Zealand short tussock grassland. *Biological Invasions*, **7**, 195–211.
- Wilson, L., Sing, S.E., Piper, G.L., Hansen, R.W., De Clerck-Floate, R., MacKinnon, D.K. & Randall, C.B. (2005) *Biology and Biological Control of Dalmatian and Yellow Toadflax FHET-05-13*. USDA Forest Service, Morgantown, WV.
- Winn, A.A. & Pitelka, L.F. (1981) Some effects of density on the reproductive patterns and patch dynamics of *Aster acuminatus*. *Bulletin of the Torrey Botanical Club*, **108**, 438–445.
- Wise, M.J. & Abrahamson, W.G. (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. *American Naturalist*, **169**, 443.
- Yokomizo, H., Possingham, H.P., Thomas, M.B. & Buckley, Y.M. (2009) Managing the impact of invasive species: the value of knowing the density-impact curve. *Ecological Applications*, **19**, 376–386.

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## Supporting Information

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

**Table S1.** Sites for monitoring *Linaria dalmatica* biological control using *Mecinus janthiniformis*.

**Appendix S1.** Citizen-based sampling protocol for monitoring biological control of *Linaria dalmatica*.

**Appendix S2.** Example of *Linaria dalmatica* monitoring site.

**Appendix S3.** List of *Linaria dalmatica* monitoring personnel.