Across intermediate spatial scales, a specialist insect herbivore responds to climate and host plant size, not host density

by

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The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, a thesis/dissertation entitled:

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Abstract

Herbivory can have important consequences for plant-population dynamics, causing changes in population growth rate, abundance, local expansion, spread and even the evolution of life history and defense traits. Studies at large spatial scales such as latitudinal gradients spanning the equatorial region to the poles, have yielded broad generalizations in patterns of herbivory. At local population scales, the effects of herbivory are often context specific, limiting extrapolation. Less described in the literature is whether patterns of herbivory manifest in between these two disparate spatial scales. At intermediate, regional scales, my research indicates that patterns of herbivory that manifest in local populations are obscured. Within a regional study area, in the southern interior of British Columbia, I found *Mecinus janthiniformis,* a stem mining weevil, did not respond to host plant *(Linaria dalmatica)* density across sites, but rather to host size. At 36 of the 39 sites sampled, herbivores were found to distribute themselves according to host plant density within populations. The direction of this effect however varied by site, resulting in no pattern at the regional scale. In conjunction with earlier research, my results suggest plant populations experiencing herbivory in different spatial patterns (i.e. more herbivory in high or low density patches) may result in different outcomes for plant population spread and persistence over time.

Lay Summary

This project aims to understand how insect herbivores distribute themselves among their host plants, and how this distribution may change with environmental conditions. Research indicates that insect herbivores show different responses to host plant density, sometimes occurring in higher numbers in areas of high host plant density or other times at higher densities in low host plant density. This relationship can have consequences for the persistence and geographic distribution of host plant populations. I found within the southern interior of British Columbia, Canada, the distribution of insect herbivores in response to host plant density varies by geographic location. Insect herbivores are most responsive to host plant size within sites, and more broadly, the temperature across sites. While there was no pattern at the regional scale, more than half my sites exhibited insects being attracted to plants in low density patches.

Preface

This thesis is original, unpublished work by the author, Emily M. West. Supervision and guidance for this research was provided by Dr. Jennifer L. Williams (University of British Columbia) All research conducted on BC provincial park land and within conservation areas (including Lac du Bois Grasslands) was done with explicit permission from regional land managers. All data were collected and analyzed by the author.

Portions of this work were presented during the poster session at the Canadian Society of Ecology and Evolution annual conference (Guelph, Ontario, July 2018).

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And lastly, a sincere thank-you to Jens C. Johnson. I am incredibly grateful to have shared my graduate experience with you. If you are ever in need of a ‘boo, I’ve got you covered.

Dedication

This work is dedicated to my family: Mom, Pips, Lindsey, Michael and Haleigh. Because of you I have never had to look very far to find people I admire.

Introduction

The strength and effect of insect herbivory on plant populations varies spatially with biotic and abiotic factors (Maron et al., 2014; Myers and Sarfraz, 2016). Historically, at the broadest spatial scales, patterns of herbivory have been attributed to latitudinal gradients corresponding to generalizable trends in climate and biological interactions (Andrew and Hughes, 2005). More recent evidence however suggests that latitude explains the strength and impact of herbivory in fewer cases than previously understood (e.g. Moles et al., 2011). At finer local scales, the level of insect herbivory experienced by target plant populations can be affected by resource availability, interspecific competition and the spatial arrangement of the target and non-target plants (Grez and Prado, 2000; Blumenthal et al., 2012). Processes that influence species interactions, such as dispersal, nutrient cycling, and disturbance can operate at different spatial scales, resulting in the extent and/or the strength of herbivory changing with scale (Doak et al., 1992; Pickett and Daenasso, 1995; Thies et al., 2003; Wiens, 1989). Therefore, selecting the scale at which to study an interaction is critical. While broad scale studies do not lend themselves to understanding mechanistic drivers the way fine scale studies do, they hold the greatest promise in overcoming context-dependent results and making generalizations across populations (Wiens, 1989; Maron et al., 2014). Reconciling the coarseness of large scale generalizations with the context dependent outcomes of localized studies and experiments presents a longstanding challenge to ecology (Maron et al., 2014).

Insect herbivory can be an important catalyst for change in local plant population dynamics (Agrawal et al., 2012; Maron and Crone, 2006; Myers and Risley, 1994; Myers and Sarfraz,

2016). While insect herbivory infrequently results in plant mortality, consumption of plant material can disrupt physiological processes that alter plant vital rates which can then precipitate changes to population growth rate, distribution, abundance, evolution of defense traits, and even population expansion (Myers and Risley, 1994; Fagan et al., 2005; Maron and Crone, 2006; Agrawal et al., 2012; Reese et al., 2016). Importantly, the biotic and abiotic conditions under which insect herbivores can apply enough pressure to cause changes in plant population growth rate is highly variable across species and environments (Myers and Sarfraz, 2016; Reese et al., 2016). In cases where herbivory reduces growth or fecundity without affecting density dependent constraints on population growth rates, herbivores can supress population growth rates (Myers and Risley, 1994; Ehrlen, 1995). In other cases, if herbivory releases plants from density dependent controls, a compensatory response can be expected, resulting in a sharp episodic increase in population growth rate (Buckley et al., 2001). In addition, if herbivory does not affect the life history stage of the plant that the population growth rate is most sensitive to, then herbivory will have negligible effects on the plant population (Ehrlen, 1995; Myers and Risley, 1994). The impact of herbivory on plant distribution and spread may ultimately be driven by the spatial distribution of insect herbivores within plant populations, but little is known about such patterns at regional scales (Fagan et al., 2005; Fagan et al., 2002).

At the local scale, insect herbivores can respond to the spatial arrangement of their host plants (Root, 1973; Otway et al., 2005; Stephens and Myers, 2012). Patterns of insect herbivore distribution relative to host plant density has largely been investigated at fine scales in singular populations or experimental arrays (see Kunin, 1999; Otway et al., 2005; Root, 1973; Stephens and Myers, 2012). In an agricultural experiment, Root (1973) first characterized plant-insect

interactions in terms of plant density mediating the distribution of herbivorous insects. He found in areas of high host plant density more specialist insect herbivores occur per host plant and subsequently, more insect damage per plant than in areas of low plant density. This phenomenon was termed the resource concentration hypothesis (Root, 1973). In the intervening years, several studies have found that this outcome can vary substantially as a result of herbivore diet breadth, herbivore competition and predation, means of dispersal, and feeding guild (Kunin, 1999; Otway et al., 2005; Stephens and Myers, 2012). The converse to the resource concentration hypothesis is the resource dilution hypothesis, whereby more insect herbivores are expected on plants that are spatially isolated from conspecifics (Otway et al., 2005; Stephens and Myers, 2012). Alternatively, herbivore density can have no response to plant density (Stephens and Myers, 2012). Halpern et al. (2013), found that changes to plant traits in response to plant density can in part mediate herbivore density. Specifically, as the number of plant neighbors increased, a decrease in mean leaf length was associated with fewer insect herbivores per plant (Halpern et al., 2014).

The consequences of herbivory for plant population abundance and distribution can depend on whether insects follow the resource concentration, dilution or no relationship pattern (Stephens and Myers, 2012). In a simulation study based on *Centaurea diffusa,* an invasive weed in North America, when specialist herbivores followed the predictions of the resource concentration hypothesis, the number of *Centaurea diffusa* patches was stabilized and the rate of population decline induced by herbivory was slowed. When herbivores followed a weak resource dilution distribution, or had no relationship with plant density, the rate of plant population decline was accelerated (Stephens and Myers, 2012).

Despite the prolific variation in plant-insect interactions, herbivory plays an important role in invasive species management. Biological control agents are commonly used as a cost-effective way of managing ecologically and economically damaging plants. Biocontrol approaches are often used in systems where the extent of infestation surpasses the ability of land managers to control it using conventional chemical and mechanical methods. Weed-biocontrol complexes have also emerged as biologically tractable systems for which ecological research questions can be applied (Svenning et al., 2014). As economically important species, invasive weeds are typically well studied. This allows managers to target control measures but also enables researchers to ask ecologically motivated questions. Specifically, the relationship between invasive weeds and biological control agents is one that allows for the examination of the effects of herbivory on plant populations across the introduced range of both plant and insect. The underlying assumption of biological control agents is that consumption of plant material negatively affects plant population growth and persistence (Marchetto et al., 2014). Specialist insects are chosen for introduction in the plant's introduced range after being identified as having some measurable effect on plant populations in the native range and after extensive host-diet breadth testing (Kunin, 1999; Myers & Risley, 1994). These systems enable researchers to utilize plant-insect interactions that are already well studied (see Kunin, 1999). Furthermore, the restricted diet of the biocontrol agent ensures that variation in herbivory levels introduced by non-target feeding will be minimal.

To address how insect herbivory varies across a regional scale, and the underlying abiotic and biotic drivers of this variation, I examined the interaction between *Linaria dalmatica* (Dalmatian

toadflax), an invasive weed widely distributed in North America, and the specialist stem-mining weevil, *Mecinus janthiniformis* that has been introduced as a biological control. I focused my study on the southern interior of British Columbia, Canada. Using this system, I examined the following questions: 1) Does the distribution of herbivores within plant populations depend on plant density within a site, and does this relationship vary across the broader region? 2) What are the biotic and abiotic factors that contribute to the anticipated variation in herbivores abundance across sites? Due to the broad sensitivity of insects to temperature and the importance of precipitation for plants, I predict temperature and precipitation to be the primary climatic drivers of the variation in each taxa's density respectively. 3) To what extent is plant fecundity negatively affected by herbivore load, and does the effect of *M. janthiniformis* on fecundity vary across the region? I expect, based on earlier studies, that the fecundity of *L. dalmatica* should be negatively affected by *M. janthiniformis*.

Methods

Study System

Dalmatian toadflax, *L. dalmatica* is a perennial noxious weed that was first introduced to North America in the late 1800s (Sing and Peterson, 2011). Since its escape from cultivation, Dalmatian toadflax, hereafter referred to as toadflax, has spread throughout the U.S. and Canada and has established in landscapes similar to its native range in Eastern Europe (Kyser and Ditomaso, 2013). In its introduced range, toadflax is often found in open, rocky, well drained soils that have been recently disturbed. Growing up to 1 meter tall (Kyser and Ditomaso, 2013), it can effectively reproduce through vegetative or sexual means, with a single plant producing up

to 500,000 seeds (Robocker 1970, Vujnovic and Wein, 1996). Dalmatian toadflax is self-incompatible and relies on insect pollination for fertilization, which contributes to high genetic variation across populations (Kyser and Ditomaso, 2013). Vegetative spread occurs from lateral roots. Once a daughter plant has established from a lateral root it will form its own root system, and become independent of the mother plant (Vujnovic and Wein, 1996; Kyser and Ditomaso, 2013). The combination of high seed viability and efficient lateral spread make this plant a challenging weed to control in its introduced range (Jamieson & Bowers, 2010; Robocker, 1970; Vujnovic & Wein, 1996).

Due to its detrimental effects on native biodiversity, as well as its economic impact on agricultural landscapes, land managers in the United States and Canada have actively sought to manage toadflax populations. Along with the exclusion of native vegetation through competition and allelopathy (Vujnovic and Wein, 1996; Maron and Marler, 2008; Kyser and Ditomaso, 2013), toadflax is poor forage for wildlife and cattle (Sing and Peterson, 2011). Prolific seeding, effective lateral spread, and waxy leaves make Dalmatian toadflax resistant to traditional chemical and mechanical control methods (Jamieson and Bowers, 2010). As a result, since the 1950's a myriad of biological control agents have been introduced to control Dalmatian toadflax including leaf defoliators and seed feeding insects. One of these, *M. janthinus*, was introduced to southern British Columbia, Canada in 1994. Sourced from populations in Western Europe (Tosevski et al., 2011) it has since spread throughout the range of Dalmatian toadflax through additional intentional releases and natural dispersal. In 2011 Toševski et al., established there were two cryptic species of weevil, *M. janthinus* which prefers the close relative yellow toadflax (*L. vulgaris*), and *M. janthiniformis* which prefers Dalmatian toadflax (Hubbard, 2016). It is

nearly impossible to distinguish between the weevils without molecular testing (Tosevski et al., 2011). Given the reference to *M. janthiniformis* in the literature following this discovery, it is assumed for the purposes of this study that weevils found on Dalmatian toadflax are in fact *M. janthiniformis* (see Weed and Schwarzländer, 2014; Wildon, 2017).

M. janthiniformis is a univoltine, stem mining weevil (McClay and Hughes, 2007). Adult weevils emerge in the spring from previous year's ramets. The females find their host plants through olfactory chemical cues originating from toadflax foliage (Hubbard, 2016). Once on a host plant, adults feed on the leaves, and have marginal adverse effects on photosynthetic processes (Carney, 2003). After mating, females oviposit a single egg into the stem where the larvae undergo three instars before pupating. Larval feeding before ramet differentiation to vegetative or reproductive shoots, can reduce the number of flowering ramets produced, and continued feeding through the growing season on flowering plants can reduce seed set (Carney, 2003). After pupation in the late fall, adult weevils overwinter in the stem of their host plant. *Mecinus janthiniformis* is sensitive to low winter temperatures, which can reduce abundance in the following years. Populations appear to be quite resilient however, if the subsequent years are environmentally amenable (De Clerck-Floate and Miller, 2002).

Field Methods

In the summer of 2017 I sampled 39 sites across the southern interior of British Columbia (Figure 1). The criteria for site selection were that no management interference had occurred between sampling dates and adult weevils were present. All sites were located within 100m of primary or secondary roads and exposed to similar levels of disturbance (Appendix A). I visited

sites twice throughout the growing season (May – August). To evaluate whether the resource concentration or resource dilution hypotheses were operating in this system, I established 1-4 transects such that the transects intersected the highest and lowest density patches of toadflax. The length, orientation and number of transects was based on the spatial distribution of toadflax. During the first visit (May-June 2017), I counted the number of toadflax stems (ramets) in each 1 x 1 m^2 plot along each transect. Ramets were counted instead of genets because it was infeasible to determine connectedness without excavating each plant. At each site I sampled a minimum of 10, 1 x 1 m^2 plots and a maximum of 50 plots depending on the spatial extent of the toadflax population.

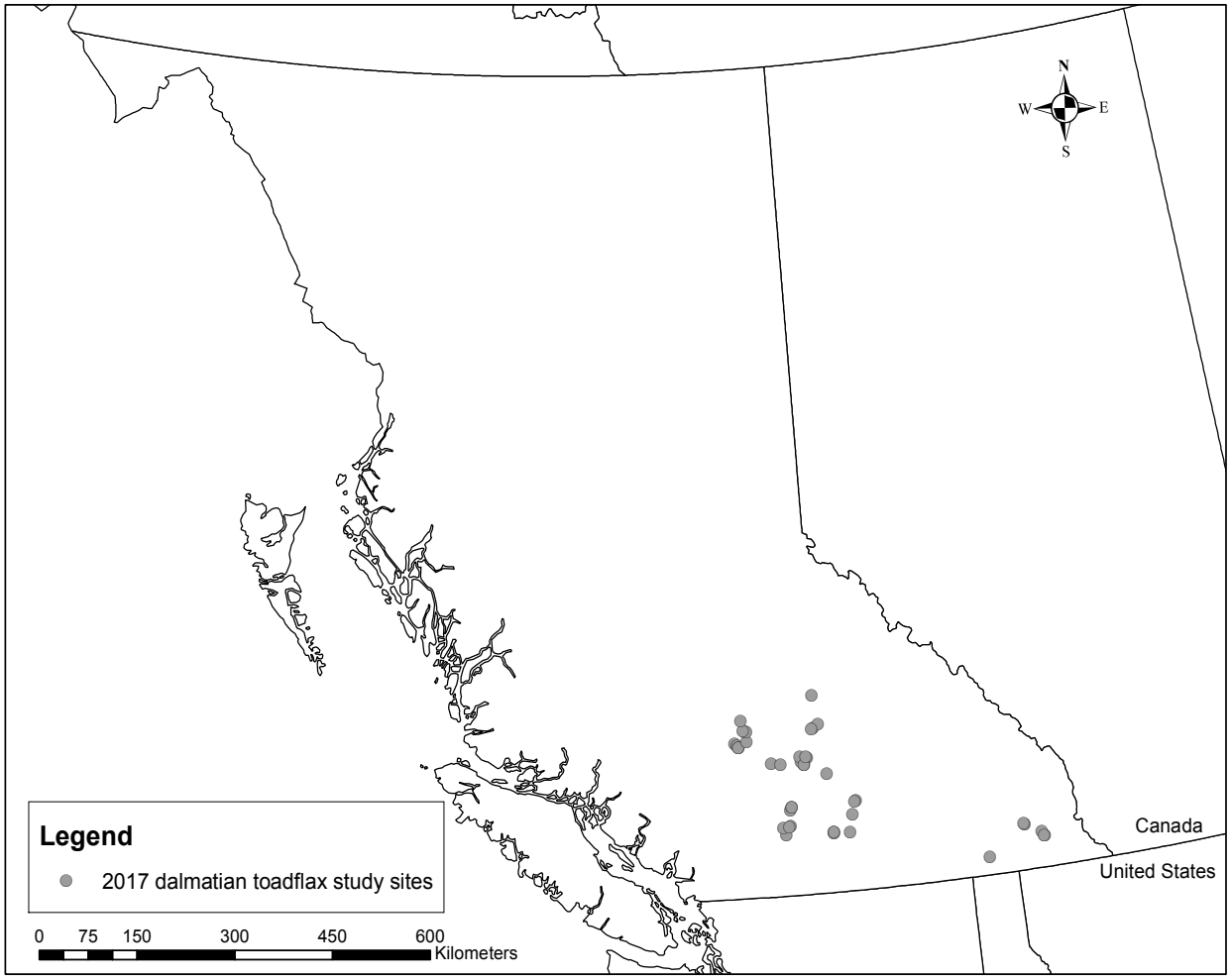

Figure 1. Locations of the 39 field sites where I surveyed for Dalmatian toadflax and *M. janthiniformis* in the southern interior of British Columbia in 2017.

During the second visit, July-August 2017, I used a systematic random approach to collect 10 ramets from the highest and lowest density plots respectively (n = 20 for each site). The first ten plants from each density type were collected regardless of their reproductive status. To ensure I had enough flowering plants to answer questions pertaining to fecundity, once the first ten plants were collected, I continued to collect the appropriate number of flowering ramets to ensure my

sample size of flowering ramets was $n = 10$ for each density type. Therefore, total number of plants collected depended on how many additional flowering stems needed to be collected to achieve this criterion. To reduce the likelihood of sampling ramets from a single genet, I selected ramets at least 10 cm away from the nearest collected stem. Prior to collecting a ramet I measured its height from the ground to the tip of the stem. I then clipped the stem at ground level and placed it in a double paper bag for transport back to the lab.

A total of 1,101 Dalmatian toadflax ramets with stem diameter > 1 cm were collected from 39 sites. Ramets with a basal stem diameter of less than 1 mm were collected, but excluded from analysis because those plants are unlikely to support the successful development of *M. janthiniformis* (*Operational Field Guide to the propagation and establishment of the bioagent Mecinus janthinus (Toadflax stem-mining weevil),* 2000). For questions not pertaining strictly to themes of reproduction, only the first 10 plants sampled from each density type were used in analyses. As previously stated, once the first ten ramets were collected from each density type, *n* number of additional flowering ramets were collected so that the total number of flowering ramets collected per density type was 10.

Once stems were transported back to the lab, they were stored in a refrigerator at 4.4°C to arrest weevil development and feeding until stems could be dissected (De Clerk-Float, personal communication, 2017). In addition to measurements taken in the field I measured the basal stem diameter of each ramet and counted the number of flowers and seed heads each stem produced. I dissected each ramet longitudinally and counted the number of weevils residing in each stem. The weevils were then placed in a labelled plastic bag and placed in a freezer for storage.

In addition to the biological data collected at each site, I also recorded slope, aspect and elevation. I obtained 14 climate variables from climatewna.com, a web based application with detailed climate data interpolated from historical weather station data (see Appendix B and C) (Wang et al., 2016).

Statistical Analysis

To determine whether weevil density per ramet per plot varied by site, I used simple linear regressions with fixed effects only. The response variable, weevil density per ramet, was log transformed to meet linear model assumptions of homoscedasticity and normality. The model with site as a fixed effect was compared to the intercept only model using a log likelihood ratio test. To determine whether plant density (per 1 m^2) varied by site I used the same method but instead of using only data from plots ramets were collected from, I used the full data set which included ramet densities for all plots within a site, thus increasing the number of observations per site. The response variable, number of ramets per square meter was transformed using square root to meet linear model assumptions of homoscedasticity and normality.

I used linear mixed effects models to address my research questions pertaining to the distribution of weevils and ramet fecundity. To examine abiotic and biotic factors that might influence the relationship between weevil density (quantified as mean number of weevils per plant within a 1 m^2 plot) and host plant density (quantified as ramet density per plot), I selected 11 plausible explanatory variables *a priori* to be used in the models (Appendix B). I used two host-plant variables as potential predictors of weevil density in addition to ramet density per plot: mean

basal diameter per ramet per plot and mean height per ramet per plot. Due to the sensitivity of weevils to temperature I used a number of temperature-based predictors which outnumbered the other climate variables (De Clerck-Floate & Miller, 2002). Abiotic predictors were: longitude, latitude, elevation, maximum summer temperature, minimum summer temperature, minimum winter temperature, mean annual temperature and mean annual precipitation. First, I refined the number of potential explanatory variables to determine which variables might contribute to variation in mean weevil density per plant per plot using a series of models with mean weevil density as the response, and one of the 11 predictor variables, with site treated as a random effect. I evaluated whether each of the 11 predictors significantly improved the intercept only model using a log-likelihood ratio test (Table 1). From the resultant 8 significant predictor variables, the dredge() function in R was used to fit all combinations of variables containing up to 5 variables per model (Barton, 2018). I used Pearson's product moment correlation to assess the level of multicollinearity between model parameters (Appendix D). To be considered further, a model could not contain any variables with $|r| > 0.7$ (Graham, 2003; Dormann et al., 2013).

Site was explicitly added to the models as a random effect to account for other unexplained variation that could be attributed to the site level, and variation at the plot level was accounted for in the final error term of the models. Models were fit using maximum likelihood. I log transformed the response variable, mean number of weevils per ramet per plot, to meet linear model assumptions of normality and reduce heteroscedasticity. I averaged metrics taken at the ramet level (height, basal diameter, number of flowers, and weevil density) across plots to reduce the hierarchy from ramets within plots within sites, to simply plots within sites. The result was 222 observations at the plot level.

I used Akaike's information criterion (AIC) to identify the model that best explained the data (Burnham and Anderson, 2002). AIC selection was favored over log-likelihood because it assigns a penalty for superfluous explanatory variables. I ranked models from lowest to highest AIC; models with a delta AIC < 2 ($\Delta_I < 2$) are listed in Table 4. In addition to AIC, Pseudo R^2 was also used to compare models based on fit:

$$\text{Psuedo } R^2 = 1 - \left(\frac{SSE}{SSY}\right) = 1 - \left(\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2}\right) \quad (1)$$

where *SSE* is the sum of squared error and *SSY* is the sum of squared y, whereby both SSE and SSY have been back transformed so they are in original units of y (Orelien and Edwards, 2008).

To evaluate the effect of mean weevil density per plant within a plot on toadflax fecundity, I again used linear mixed effects models. For this analysis I used data only from flowering plants. The response variable, mean number of flowers produced per ramet per plot, was log transformed to meet linear model assumptions of homoscedasticity. I used a similar approach to above, using a stepwise approach of testing each simple linear regression of the a-priori selected variables to the intercept only model predicting mean number of flowers produced (see Table 6 for *a priori* variables). Using a likelihood ratio test, only variables with a p-value < 0.05 were retained for further investigation (Table 3). All remaining predictor variables were assembled into a global mixed effects model with site as a random effect. The dredge() function was used to rank models with every combination of variables. Dredge() parameters were constrained to

models containing combinations of 1-4 predictor variables. Models were fit using maximum likelihood.

All statistical analyses were conducted in R, version 3.3.2 (2018).

Results

I found no significant relationship between Dalmatian toadflax (*L. dalmatica*) density and the density of the stem mining weevil *M. janthiniformis* (Table 1), which yields no support for either the resource concentration or resource dilution hypotheses in this region. Instead of being explained by plant density, the best supported models explaining variation in weevil density across sites included mean basal diameter (per 1 m^2 plot), longitude of the site and either mean annual temperature, minimum summer temperature or elevation (Table 2). All three models were indistinguishable from the top model (delta AIC < 2) and avoided the problem of multicollinearity among environmental variables (Appendix D; see Appendix E for all models with delta AIC <2). All three models predict more weevils to occur on plants with larger basal stem diameter, that are located further east in the study region (Figure 2). Mean annual temperature and minimum summer temperature are both strongly negatively correlated to elevation (Appendix D). The three variables that varied between models, mean annual temperature, minimum summer temperature, and elevation all indicate that more weevils occur at warmer sites. The model including elevation had the highest pseudo R^2 (pseudo $R^2 = 0.465$), explaining at least 5% more of the variation in weevil density than either of the other two models (Table 2). An ad hoc Pearson's product-moment correlation confirms there is no correlation

between ramet size, measured as basal stem diameter, and ramet density per meter^2 (cor = 0.054, p = 0.423), further validating the absence of a relationship between weevil density and *Linaria* density.

Table 1. The 11 explanatory variables selected *a priori* to predict mean number of weevils per ramet per 1m^2 plot. Log-likelihood ratio tests were used to compare simple linear regressions of each potential explanatory to the intercept-only model. The 8 variables with p-values < 0.05 are in bold.

Model Parameter	AIC	X^2	p-value
Intercept only	535.67		
Mean basal stem diameter (cm)	441.73	95.94	**<0.0001**
Mean stem height (cm)	495.90	41.77	**<0.0001**
Maximum summer temperature (ºC)	508.66	29.02	**<0.0001**
Elevation (m)	509.78	27.89	**<0.0001**
Mean annual temperature (ºC)	510.74	26.93	**<0.0001**
Minimum summer temperature (ºC)	518.43	19.24	**<0.0001**
Minimum winter temperature (ºC)	521.71	15.97	**0.0001**
Longitude (decimal degrees)	529.27	8.41	**0.0037**
Latitude (decimal degrees)	535.75	1.92	0.166
Mean annual precipitation (mm)	536.56	1.11	0.291
Stem density (ramets/ m^2)	537.24	0.44	0.509

Table 2. Coefficient estimates for the top 3 models predicting mean weevil density per ramet per 1m^2 plot.

Mean stem diameter	Longitude (decimal degrees)	Mean annual temp.	Elevation (m)	Min. summer temp.	delta AIC	Pseudo R^2
0.509	0.121	0.248	-	-	0.00	0.41
0.521	0.138	-	-	0.19677	1.11	0.40
0.499	0.140	-	-0.00148	-	1.39	0.47

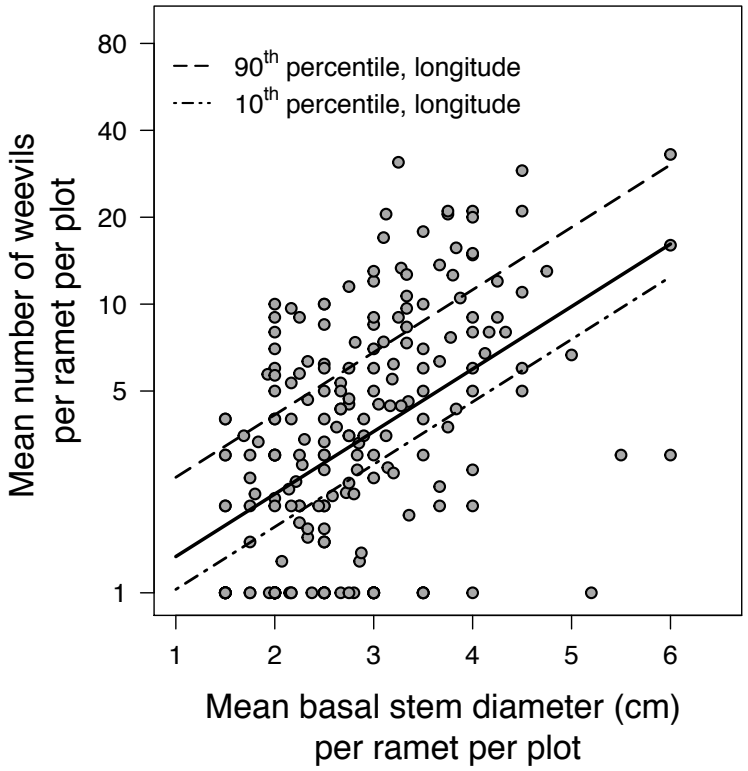

Figure 2. Mean number of weevils per ramet per m^2 in response to mean basal stem diameter. Dashed lines indicate the 10^{th} (western edge) and 90^{th} (eastern edge) percentile of longitude in the dataset.

I found no evidence that weevil load (number of weevils per ramet) affects the number of flowers produced per ramet in plots across sites (Table 3). This was true whether weevil density was considered a numeric or categorical variable (presence/absence). Instead, plant size, as measured by height, was the biological factor that best explained the number of flowers produced by a ramet. As expected, taller plants produce more flowers (Figure 3). Mean annual temperature, mean annual precipitation, and mean summer temperature all significantly improved the intercept only model. Given that mean annual temperature and mean summer temperature are significantly correlated ($r = -0.978$; p-value $< 2.2e^{-16}$) only mean annual temperature was considered as a possible predictor variable in the global model. Mean annual

temperature and mean annual precipitation were negatively correlated (r = - 0.317; p-value < 0.001). The best supported model indicated that plant fecundity responds favorably to cooler, wetter conditions. The estimated coefficients for this model were: mean height = 0.0291, mean annual precipitation = 0.0015, and mean annual temperature = -0.116. This was the only model with delta AIC <2, this model had a pseudo R^2 of 0.380.

Table 3. AIC and Chi-squared (X^2) values from log-likelihood ratio tests of *a priori* selected variables used to predict mean number of flowers produced per ramet withinin a 1m^2 plot. The 5 simple linear regressions with significant predictor variables compared to the intercept-only model are in bold.

Model parameter	AIC	X^2	p-value
Intercept only	534.44		
Mean stem height	445.38	-91.06	**<0.0001**
Weevil presence/absence^{x}mean height	444.94	95.50	**<0.0001**
Mean summer temp.	532.11	4.33	**0.038**
Mean annual temperature	532.39	4.04	**0.044**
Mean annual precipitation	532.42	4.01	**0.045**
Mean spring precipitation	532.63	3.80	0.051
Elevation	532.79	3.65	0.056
Mean winter precipitation	532.88	3.56	0.059
Mean weevil density	534.89	1.54	0.214
Latitude	536.02	0.41	0.520
Mean summer precipitation	536.43	0.00	0.604
Longitude	536.33	0.10	0.749
Weevil presence/absence	536.36	0.07	0.787

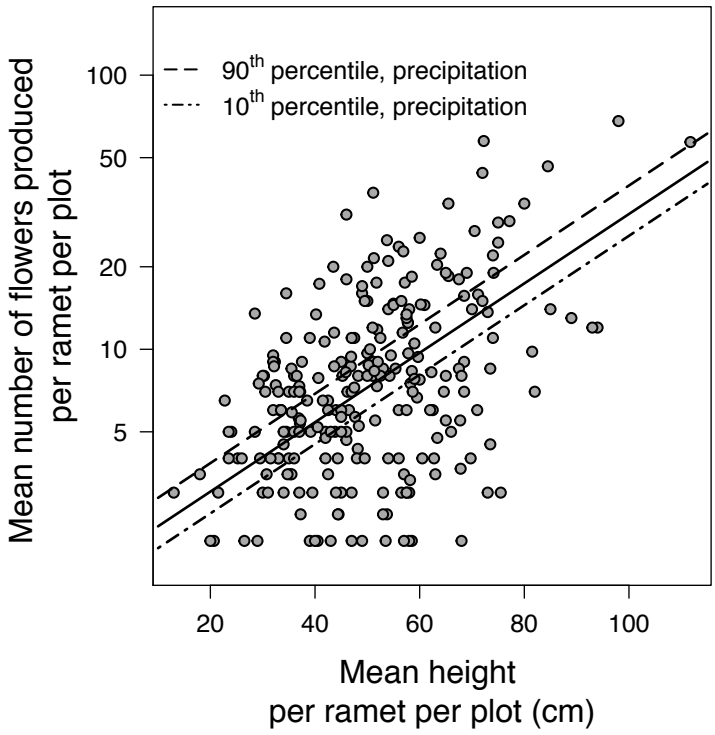

Figure 3. Number of flowers produced per ramet in response to ramet height. Dashed lines indicate the 10th and 90th percentile for mean annual precipitation (mm).

Weevil density per ramet varied significantly between the 39 sites ($F_{38,637} = 7.101$; $P < 2.2e^{-16}$), although none of the sites in the study region were close to peak weevil densities earlier reported in the same region (Van Hezewijk et al., 2010) as measured by weevils per centimeter of ramet (Figure 4). By maximizing the number of sites visited I was constrained with respect to within site sampling, and thus the sample sizes per site were too low to per perform rigorous statistical analyses on within site patterns. A visual comparison suggests that the mean number of weevils per ramet differed between high and low-density plots of toadflax at 36 of the 39 sites, but the direction of the effect varied across sites (Figure 5). At 12 sites, ramets from high density plots had more weevils; at 24 sites, ramets from low density plots had more weevils; and 3 sites had

no difference. Plant density per meter square also varied significantly by site ($F_{38,787} = 5.885$; $P < 2.2e^{-16}$).

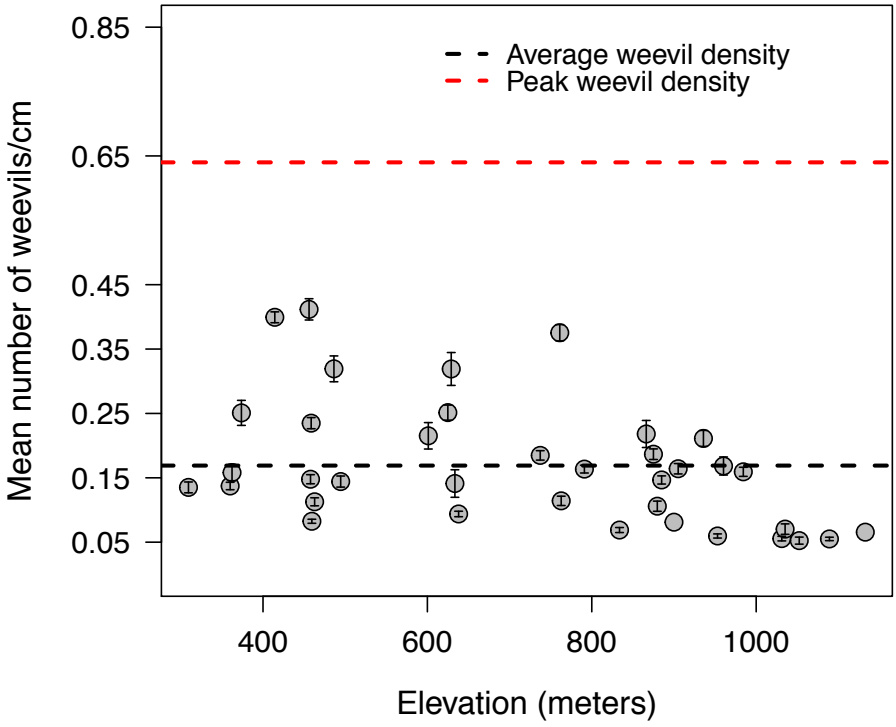

Figure 4. Mean number of weevils/centimeter for each site. Sites are arranged by elevation. Red line = peak weevil density established by Van Hezeweijk et al., 2010; black line = mean weevil density/centimeter across all sites.

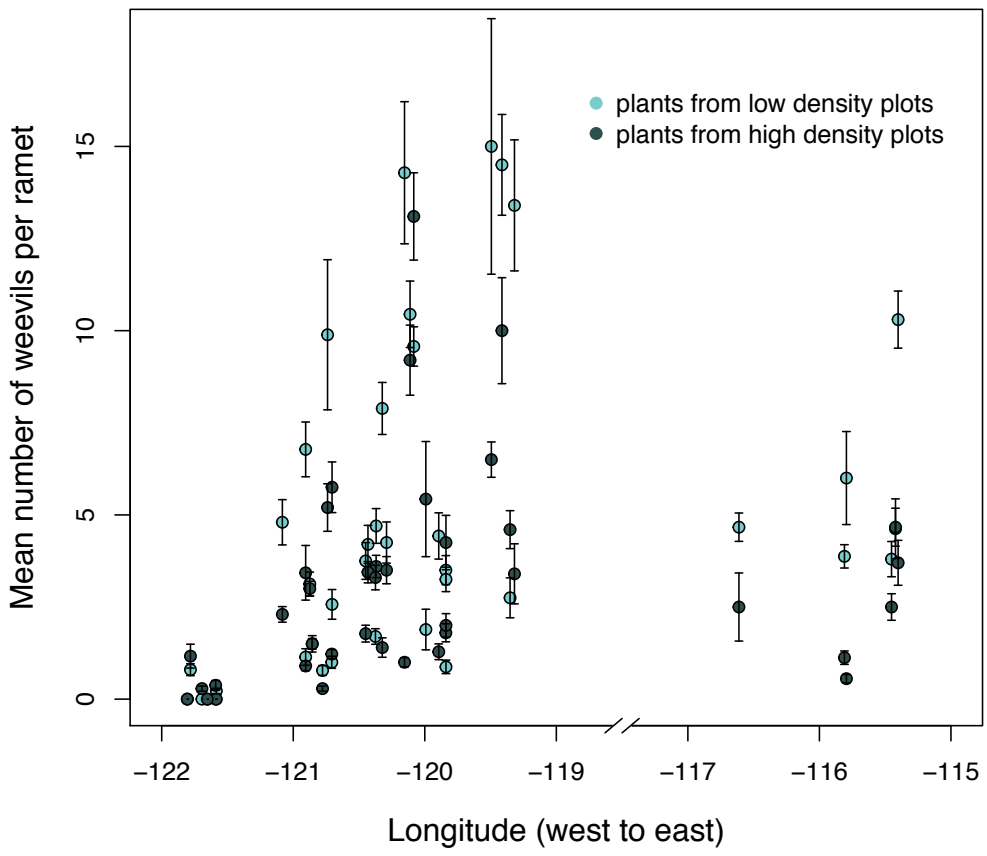

Figure 5. Mean number of weevils per plant by density type (light blue = low density plots, dark green = high density plots). Error bars indicate standard error of the mean; the number of plots per density at each site ranged from 1 – 4.

Discussion

Increasingly, spatial scale is recognized as playing a critical role in the observed patterns of species interactions such as herbivory (Thies et al., 2003; Davies et al., 2005; Louthan et al., 2018). As the scale of the study is broadened or narrowed, different patterns emerge or become obscured. In the Dalmatian toadflax-*Mecinus* system, herbivores did not respond to plant density in a predictable way across all 39 sites (Table 1). Instead, there was a high degree of variation in

the spatial distribution of herbivores within sites, with more weevils occurring in plots with higher plant densities at some sites and lower plant densities at others (Figure 5). The absence of a relationship between weevil density and plant density at the regional scale is attributable to this high degree of variation in how herbivores are distributed within each site. In addition, there was no discernable effect of weevil density on the fecundity of *L. dalmatica* across the study area.

Ramets of *L. dalmatica* that attract more female weevils have a higher number of weevil offspring emerging the following spring (Carney, 2003). This suggests that more females are attracted to larger plants. Female weevils find their host plants using chemical signals, including chemical volatiles and iridoid glycosides, which are both produced by the leaves of Dalmatian toadflax (Hubbard, 2016; Jamieson and Bowers, 2012). If larger plants produce more leaves, then larger plants may produce higher levels of important chemical cues attracting more female weevils. However, in at least one study, iridoid glycoside concentrations in Dalmatian toadflax were negatively correlated with injury caused by *M. janthiniformis* (Jamieson and Bowers, 2012). In general, there is a high amount of genetic and abiotic variation between populations of Dalmatian toadflax populations, which contribute to spatial and temporal variation in the production of chemical defenses (Jamieson and Bowers, 2010; Kyser and Ditomaso, 2013). The underlying mechanism that attracts more weevils to larger plants remains unknown. My results in conjunction with Carney's (2003) indicate that larger plants attract more female weevils which suggests future studies are needed to determine how weevils are able to distinguish between plant size.

The abiotic drivers of weevil density across sites were temperature, elevation and longitude. At higher elevations weevils are exposed to colder, wetter conditions, which are known to be unfavorable to the development and survival of *M. janthiniformis* (De Clerck-Floate and Miller, 2002). The early onset of cold weather in the autumn at high elevation shortens the period of development for weevils to reach the over-wintering adult stage of their lifecycle. Additionally, lower winter temperatures can result in high rates of adult mortality (De Clerck-Floate and Miller, 2002). This leads to an overall reduction in adult emergence in the spring. Therefore, it is not surprising that study sites located in warmer, drier locations had more weevils than cooler, wetter sites.

There are two ways in which longitude may be explaining variation in weevil density across sites. The first way in which longitude can in part explain variation in weevil density is due to its correlation with climate (Appendix D). Temperature increases west to east across my study sites, and my results show an increase in weevil density at sites with warmer temperatures (Table 1). The second way in which longitude may explain variation in weevil density is the spatial and temporal distance sites are from weevil release locations. Eastern sites are not only geographically closer to historic release sites, they are also closer to sites of on-going weevil release programs. This allows weevils to disperse more easily to those sites located in the eastern and central portion of the study region, as well as allow the release sites to act as sources for weevil populations behaving as sinks, which is an unknown dynamic at this time (Heimpel and Asplen, 2011). To my knowledge, there are no on-going releases near the Clinton-Chasm sites, located in the far western portion of the study region (Hughes, *personal communication,* 2018). As these sites are located the farthest from weevil release sites, they will take the longest for

weevils to disperse to naturally (Heimpel and Asplen, 2011). Unlike latitude however, there is a dearth of understanding in the literature of how longitude affects herbivory. Prevailing wisdom has traditionally associated higher levels of herbivory with lower latitudes (Andrew and Hughes, 2005). However, recent research exploring the role of latitudinal gradients at different scales and across different taxa reveals that patterns of herbivory across latitude are much less distinguishable than once thought (Moles et al., 2011). In fact, Moles et al. (2011) go so far as to state that no data in the current literature support that, in general, herbivory is more intense at low latitudes. A significant limitation in comparing research on patterns of herbivory along latitudinal gradients is the breadth of approaches used to answer a variety of relevant questions, as well as the unknown importance of spatial scale (Andrew and Hughes, 2005). While my research characterizes the interaction between a single specialist herbivore and its host plant, many studies of herbivory along latitudinal gradients aggregate herbivory by feeding guild (Andrew and Hughes, 2005). Since the nature of generalist herbivore feeding is plastic in response to host availability (Kunin, 1999), I expect those studies aggregating feeding guilds to yield highly context specific results in terms of plant population persistence and abundance. That is, when generalists are included in herbivory studies, the breadth of their diet enables herbivores to readily switch target plants when one plant species becomes depleted or competition for a plant becomes too great. Thus, the results of studies including generalist species will be sensitive to the diet breadth of the insect herbivore, and the identity and number of difference plant species made available. In contrast, a specialist herbivore like *M. janthiniformis,* shows little to no plasticity in feeding, so even when exposed to different arrays of plant species, its feeding preference will remain within the *Linaria* genus and reduce the amount of expected variation in damage between studies. This discrepancy in feeding behavior

presents challenges in comparing studies and observable trends in herbivory of insects with different diet breadths (Kunin, 1999).

There are additional considerations that may help explain the variation in weevil density between sites in the study region. The first consideration is the level and frequency of disturbance that populations of Dalmatian toadflax experience. Most study sites were located in areas where cattle are periodically grazed. Despite being avoided as forage, Dalmatian toadflax is sensitive to grazing as well as disturbance during the seedling stage (Blumenthal et al., 2012). High levels of grazing and increased disturbance during seedling development reduces plant density (Robocker, 1970; Blumenthal et al., 2012). While disturbance affects Dalmatian toadflax density, it is unclear how the size of plants is affected. Earlier research suggests that plant size will largely be contingent on nutrient and water availability (Jamieson et al., 2012; Weed and Schwarzländer, 2014), suggesting that disturbance affecting those key resources will lead to changes in weevil density. The second consideration potentially affecting weevil densities is the presence of parasitoids in the study region. While the full impact of parasitoids in this system is not fully understood, parasitoids are known to affect < 10% of Dalmatian toadflax stems in the field (Schat et al., 2008). If the frequency or extent of disturbance, or the attack rate of parasitoids varies across sites, both would contribute to the unexplained variation in weevil density.

Earlier studies show Dalmatian toadflax to suffer stem wilting, reduced height and supressed flowering in response to high or outbreak densities of *M, janthiniformis* (Carney, 2003; Peterson et al., 2005; Van Hezewijk et al., 2010). I found that larger plants produce more flowers, regardless of the number of weevils. One explanation of this may be that weevil densities at my

study sites have not reached peak densities of 0.64 weevils/cm of stem (Van Hezewijk et al., 2010). Jamieson et al., similarly proposed a threshold in terms of oviposition scars per centimeter of stem (2012). A minimum of 0.8 oviposition scars per centimeter were required to induce physiological damage leading to reduced growth and fecundity in their experiment (Jamieson et al., 2012). In comparison, the number of weevils/cm in ramets across sites in my study were well below these thresholds, ranging from 0.05 weevils/cm to 0.4 weevils/cm, with an average of 0.17 weevils/cm (Figure 4). The life history of Dalmatian toadflax is also likely to play an important role in the absence of a relationship between fecundity and weevil density. As a perennial plant toadflax can employ below ground resources to overcome damage caused by non-peak densities of *M. janthiniformis* (Tenhumberg et al., 2018). Regardless of its perennial growth habit, the long-term population stability of Dalmatian toadflax is not likely to be driven by the number of seeds produced because this plant is more often site limited than seed limited (Robocker, 1970; Vujnovic and Wein, 1996). This suggests the impact of *M. janthiniformis* on the fecundity of Dalmatian toadflax is less critical to the management of toadflax populations than its effect on other life history traits, such as those relating to growth and survival.

The number of flowers produced per ramet of Dalmatian toadflax responded favorably to cooler, wetter conditions in the study area. Those plants located at cool sites, receiving more annual precipitation produced more flowers, regardless of the number of weevils (Table 3). Wet periods can increase nutrient availability, and have a positive effect on plant growth (Weed and Schwarzländer, 2014), thus making plants more resilient to herbivory (Jamieson et al., 2012). This would suggest that plants located in warm, dry climates are less capable of overcoming physiological stress induced by herbivory. Furthermore, I found that plants located at higher

elevations, in wetter climates were exposed to fewer herbivores than those located in warm dry climates, allowing them to escape the full impact of higher herbivore densities.

For systems where there is no link between herbivore distribution and plant density, such as the toadflax-*Mecinus* system, it is a complex task to characterize the effect of herbivory on plant population dynamics such as local persistence and spread. This is because the way in which insect herbivores distribute themselves within patches of expanding populations has important consequences for the way in which a population expands across a landscape (Fagan et al., 2005). For example, in populations of lupine on Mt. St Helens, where plant spread is driven from a distinguishable edge of patchy, low density plants, Fagan et al. (2005) found that herbivores can slow the rate of spread by aggregating on those isolated edge plants and inducing an Allee-like effect. My results indicate that across populations, the aggregation of herbivores is not predictable based on plant density alone, thus complicating our ability to model how herbivores may affect the rate of plant population spread. If herbivores respond strongly to plant size, as in the case of *M. janthiniformis*, understanding the factors that drive the distribution of large plants will be crucial in understanding how those herbivores affect spread.

Mecinus janthiniformis is largely considered a successful biological control of *L. dalmatica*. Not only has the insect established and spread throughout the study area, in general plant population densities are reported to be lower than those prior to weevil release in the 1990s (Van Hezewijk et al., 2010). The successful suppression of toadflax population abundance may be attributable to my result that weevils fail to respond to plant density. Stephens and Myers (2012) found that when herbivores are weakly associated with low plant densities (resource dilution), or there is no

relationship with plant density, the rate of plant population decline is accelerated, as compared to a resource concentration distribution where patch dynamics can dampen the effect of herbivores on plant abundance. As weevils distribute themselves ubiquitously throughout a population, emerging patches of plants are unable to escape herbivore pressure. Future biological control efforts may benefit from identifying biological control agents that exhibit weak or no preference to plant density within populations.

The primary limitation of my study is that the data only cover one growing season and a single weevil generation. Answering questions of fecundity and long-term survival are particularly challenging for perennial plants, where below ground resources enable plants to withstand levels of herbivory in one or more growing season (Tenhumberg et al., 2018). Furthermore, following a single insect generation can fail to account for cyclical population abundance dynamics, which can for *M. janthiniformis* occur in 7-8 year cycles (Van Hezewijk et al., 2010). Svenning et al. (2014) pointed to the benefit of using invasive species as study systems to investigate questions of species interactions. While invasive species do present emerging species interactions, and therefore allow for the observation of how interactions evolve through time, they also present limitations. I encountered many challenges in obtaining population records for toadflax infestations, making it impossible to produce conclusive evidence that the patterns (or lack there-of) I observed are persistent through time, are newly emerging or simply transient in response to changing environmental conditions. Once biological controls are introduced to a plant population, frequently there is very little follow-up other than presence/absence surveys and re-releases in subsequent years (De Clerk-Floate, *personal communication*, 2018). This is a missed opportunity for ecologists interested in how the spatial distribution of herbivores change over

time and how these changes affect plant population dynamics including increase, spread, and distribution. It remains unclear how transient dynamics, like those of newly introduced populations with unstable stage structures relate to the outcome of stable population dynamics (Iles et al., 2016). This introduces yet another complexity to predicting the long-term effect of species interactions on population dynamics such as population growth rates once populations have reached stable distributions.

While species interactions including herbivory remain a complex topic because of the inherent variation that occurs across different spatial and temporal scales, studies like this can help identify at what scale variation exists and how that variation can obscure patterns at other scales. In the case of my results, there was high variation in herbivore distribution in relation to plant density in local populations. This resulted in the absence of any observable patterns at the regional scale. While the absence of a pattern can be anticlimactic for a researcher, we know from earlier research like that of Stephens and Myers (2012), the absence of herbivores responding to plant density, can have significant impacts on the outcome of plant abundance and population persistence. In concert with Stephens and Myers (2012), my results support earlier assertions that *M. janthiniformis* successfully controls Dalmatian toadflax at the regional scale by being ubiquitously distributed throughout plant populations regardless of plant density. Furthermore, my results predict that *L. dalmatica* suppression will be highest in warmer drier locations, where herbivores are more abundant and environmental conditions are more favorable to weevil development and less favorable to *L. dalmatica* growth.

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APPENDICES

Appendix A Field site details

Site information for each of the 39 sites used in the analysis of weevil density and flowering production of Dalmatian toadflax.

*Adjacent road type refers to primary (paved highway) and secondary (logging, axis and dirt roads) roads.

Site number	Location	Latitude	Longitude	Elevation (m)	Slope	Aspect	Adjacent road type*	Soil texture	Soil drainage	Dominant vegetation type	BEC classification
1	Brookmere transfer station	49.81359028	-120.8720608	953	7	206	secondary	sandy loam	well drained	non-native perennial grasses	Interior Douglas-fir
2	Kane Valley rd	49.92736639	-120.7526972	1,031.20	0	NA	secondary	sandy loam	well drained	non-native perennial grasses	Interior Douglas-fir
3	Kane Valley rd hwy intersection	49.91443694	-120.9056411	1,031.20	20	348	primary	silt loam	well drained	non-native perennial grasses, native shrub	Interior Douglas-fir
4	Kane Valley rd, Niccola Ranch	49.92273056	-120.7774653	1035.2	0	NA	secondary	sandy loam	rapidly drained	mix of native and non-native forbs	Interior Douglas-fir
5	Merritt FSR/Coquihalla hwy	50.13504028	-120.7392383	629	18	107	primary	sandy loam	well drained	mix of native and non-native perennial grasses	Bunchgrass
6	Merritt FSR	50.17568694	-120.7069994	833.75	3	205	secondary	silt loam	well drained	ponderosa pine, annual native grasses	Interior Douglas-fir
7	Upper Merritt FSR	50.18052389	-120.7050981	885	5	217	secondary	silt loam	well drained	ponderosa pine, annual native grasses	Interior Douglas-fir

Site number	Location	Latitude	Longitude	Elevation (m)	Slope	Aspect	Adjacent road type*	Soil texture	Soil drainage	Dominant vegetation type	BEC classification
8	Okanagan Mtn. FSR	49.78864472	-119.4939317	624.89	7	186	secondary	sandy loam	rapidly drained	mix of perennial shrubs and annual forbs and herbs	Interior Douglas-fir
9	Kekuli Bay	50.20212583	-119.3182297	485	29	109	primary	loam	well drained	mix of non-native perennial grasses and native forbs	Interior Douglas-fir
10	Bailey Rd	50.18333	-119.3515986	457.81	0	NA	primary	sandy loam	well drained	non-native perennial and annual grasses	Interior Douglas-fir
11	Glenmore Rd	50.01436111	-119.4134175	455.19	29	55	primary	silt clay	moderately well drained	non-native perennial and annual grasses	Ponderosa Pine
12	Peachland FSR	49.80735278	-119.8401831	984.35	22	254	secondary	sandy loam	rapidly drained	mix of non-native annual and perennial forbs	Interior Douglas-fir
13	Lower Brenda Main Rd	49.79297167	-119.8389761	881	5	252	secondary	silt loam	well drained	mix of non-native annual and perennial forbs	Interior Douglas-fir
14	Upper Brenda Main Rd	49.79992889	-119.8389831	935.85	6	268	secondary	silt loam	well drained	mix of non-native annual and perennial forbs	Interior Douglas-fir
15	Barnhartvalle Rd	50.57917828	-119.8939639	638	4	190	secondary	loam	well drained	non-native perennial and annual grasses	Interior Douglas-fir
16	Palmer Forsythe Rd	50.81826167	-120.2909192	361.56	18	272	primary	silt loam	well drained	non-native perennial and annual grasses	Ponderosa Pine

Site number	Location	Latitude	Longitude	Elevation (m)	Slope	Aspect	Adjacent road type*	Soil texture	Soil drainage	Dominant vegetation type	BEC classification
17	Barriere Lakes Rd	51.20549444	-120.1119106	457.07	25	182	primary	sandy loam	rapidly drained	mix of non-native annual and perennial forbs and grasses	Interior Douglas-fir
18	Boetrell Creek Rd	51.24566111	-119.9920125	633.48	7	234	secondary	NA	NA	mix of non-native annual and perennial forbs	Interior Douglas-fir
20	Juniper Beach	50.77966111	-121.0827539	308.07	4	210	primary	sandy loam	rapidly drained	sage brush dominant	Bunchgrass
21	Savona	50.75889722	-120.8743361	362.4	7	78	primary	loamy sand	well drained	non-native perennial grasses	Bunchgrass
22	Clearwater	51.64100222	-120.0837767	412.82	10	146	primary	NA	NA	mix of non-native annual and perennial forbs	Interior Douglas-fir
23	Westsyde Rd	51.1905	-120.1540486	375.26	9	80	secondary	sandy loam	well drained	mix of non-native annual and perennial forbs	Interior Douglas-fir
24	Noble Lake Rd	50.834946	-120.32321	487.09	22	221	secondary	sandy loam	well drained	sage brush dominant, native perennial forbs	Ponderosa Pine
25	Latigo Rd	50.73220778	-120.3699114	461.1	4	79	secondary	sandy loam	rapidly drained	sage brush dominant, native perennial forbs	Bunchgrass
26	Lac du Bois	50.77373639	-120.4320328	790.91	21	47	secondary	sandy loam	well drained	native perennial grasses	Bunchgrass

Site number	Location	Latitude	Longitude	Elevation (m)	Slope	Aspect	Adjacent road type*	Soil texture	Soil drainage	Dominant vegetation type	BEC classification
27	Mqueen Lake	50.83172028	-120.4494369	968.973	22	207	secondary	loamy sand	moderately well drained	mix of native annual and perennial forbs	Interior Douglas-fir
28	Lac du Bois enterence	50.72166778	-120.3750875	458.33	16	5	secondary	sandy loam	well drained	sage brush dominant, native perennial forbs	Bunchgrass
30	Middle high bar Rd	51.04675889	-121.8052144	1220.25	41	231	secondary	silt loam	well drained	native and non-native perennial forbs	Interior Douglas-fir
32	Downing Park	51.00855889	-121.7815883	1063.72	10	109	primary	loamy sand	moderately well drained	native and non-native perennial grasses	Interior Douglas-fir
33	Clinton Power Station	51.08116981	-121.5898292	900	1	97	primary	loamy sand	moderately well drained	non-native perennial forbs and grasses	Interior Douglas-fir
35	Paradise Meadows	51.21646417	-121.5847653	1132.74	0	NA	secondary	sandy loam	rapidly drained	non-native perennial and annual forbs and grasses	Interior Douglas-fir
36	Big bar aspen grove	51.240035	-121.6534897	1122.78	13	83	secondary	silt loam	moderately well drained	native forbs	Interior Douglas-fir
37	Chasm, BC	51.37096917	-121.6941844	1089.12	0	NA	secondary	sandy loam	rapidly drained	native and non-native grasses	Interior Douglas-fir
38	Rosicky Rd	49.41630417	-115.4016722	761.06	3	247	secondary	loam	rapidly drained	native and non-native grasses	Interior Douglas-fir
39	Bull River	49.47372944	-115.4518031	762.22	42	205	secondary	NA	NA	ponderosa pine, non-native grasses	Interior Douglas-fir
40	Mission-Wycliffe Rd	49.61809917	-115.8096314	903.04	15	354	secondary	loam	well drained	ponderosa pine, non-native grasses	Ponderosa Pine

Site number	Location	Latitude	Longitude	Elevation (m)	Slope	Aspect	Adjacent road type*	Soil texture	Soil drainage	Dominant vegetation type	BEC classification
41	Mission-Wycliffe Rd 2	49.61809917	-115.7948106	866.3	3	164	secondary	NA	NA	ponderosa pine, non-native grasses	Ponderosa Pine
42	Kootenay Lake	49.23607139	-116.6117614	600.76	0	NA	primary	sandy loam	well drained	ponderosa pine, non-native grasses	Interior Cedar -- Hemlock
44	Wardner Provincial Park	49.41908889	-115.4216403	737.3	3	65	secondary	NA	NA	native and non-native grasses	Interior Douglas-fir

Appendix B Predictor variables of weevil density
Biotic and abiotic variables selected *a priori* to predict mean weevil density per ramet per $1m^2$ plot.

Biotic Factors	**Abiotic Factors**		
Plant characteristics	Site characteristics	Seasonal climate variables	Annual climate variables
Mean* stem diameter (cm) Mean stem height (cm) Stem density (ramets/ m^2)	Elevation (m) Longitude (decimal degrees) Latitude (decimal degrees)	Maximum summer temperature (ºC) Minimum summer temperature (ºC) Minimum winter temperature (ºC)	Mean annual temperature (ºC) Mean annual precipitation (mm)

*Measurements taken at the ramet (stem) level were averaged across plots and represents mean per ramet (stem) within a $1m^2$ plot.

Appendix C Predictor variables of flower production

Biotic and abiotic variables selected *a priori* to predict mean number of flowers produced per ramet. Variables unique to this analysis are in bold.

Biotic Factors	**Abiotic Factors**		
Plant characteristics	Site characteristics	Seasonal climate variables	Annual climate variables
Mean* stem height (cm) Mean weevil density (weevils/ramet)	Elevation (m) Longitude (decimal degrees) Latitude (decimal degrees)	**Mean summer temperature (ºC)** **Minimum spring precipitation (mm)** **Minimum winter temperature (mm)** **Mean winter precipitation (mm)**	Mean annual temperature (ºC) Mean annual precipitation (mm)

*Measurements taken at the ramet level were averaged across plots and represents mean per ramet within a $1m^2$ plot.

Appendix D Correlation matrix of predictor variables

Correlations between the environmental variables used in the models exploring the relationship between weevil density and host plant density. Correlations greater than |r| > 7, the accepted threshold for high correlation between variables in multivariate regressions, are bold (Graham 2003).

Model Parameters	Elevation	Mean stem diameter	Mean height	Longitude	Max. summer temp.	Min. winter temp.	Mean annual temp.	Min. summer temp.
Elevation (m)	-	-0.17*	-0.11*	-0.22*	**-0.96***	**-0.73***	**-0.94***	**-0.85***
Mean† stem diameter (mm)	-	-	0.69*	-0.02	0.13*	0.065	0.1	0.024
Mean height (cm)	-	-	-	0.14*	0.052	0.025	0.042	0.01
Longitude (decimal degrees)	-	-	-	-	0.44*	0.15*	0.31*	0.23*
Max. summer temp. (ºC)	-	-	-	-	-	0.64*	**0.91***	**0.82***
Min. winter temp. (ºC)	-	-	-	-	-	-	**0.89***	**0.91***
Mean annual temp. (ºC)	-	-	-	-	-	-	-	**0.96***
Min. summer temp. (ºC)	-	-	-	-	-	-	-	-

*Indicates a significant relationship at $\alpha = 0.05$. For relationships without *, |r| = 0.
†Measurements taken at the ramet level were averaged across plots and represents mean per ramet within a $1m^2$ plot.

Appendix E Coefficient estimates for models predicting weevil density

Coefficient estimates for top models (delta AIC < 2) explaining variation mean weevil density per ramet (log transformed) across sites. Models with predictor variables having correlations below |r| < 7 are in bold (Graham 2003).

Model number	Mean* stem diameter	Longitude (decimal degrees)	Mean annual temp.	Elevation (m)	Min. summer temp.	Max summer temp.	Min. winter temp.	Mean height	delta AIC	Pseudo R^2
1	**0.509**	**0.121**	**0.248**	**-**	**-**	**-**	**-**	**-**	**0.00**	**0.41**
2	0.501	0.143	-	-0.00100	-	-	0.086	-	0.45	-
3	0.508	0.136	-	-0.00078	0.10882	-	-	-	0.67	-
4	**0.521**	**0.138**	**-**	**-**	**0.19677**	**-**	**-**	**-**	**1.11**	**0.40**
5	0.507	0.113	-	-	-	0.108	0.109	-	1.28	-
6	0.502	0.193	-	-0.00224	0.108	-0.188	-	-	1.38	-
7	**0.499**	**0.140**	**-**	**-0.00148**	**-**	**-**	**-**	**-**	**1.39**	**0.47**
8	0.504	0.126	0.169	-0.00051	-	-	-	-	1.54	-
9	0.512	0.125	0.178	-	0.059	-	-	-	1.77	-
10	0.496	0.122	0.248	-	-	-	-	0.001	1.91	-
11	0.509	0.123	0.229	-	-	-	0.017	-	1.95	-
12	0.515	0.117	-	-	0.141	0.064	-	-	1.98	-
13	0.508	0.118	0.235	-	-	0.011	-	-	1.98	-
Frequency†	13	13	6	5	5	4	3	1		

*Measurements taken at the ramet level were averaged across plots and represents mean per ramet within a 1 m^2 plot.
† Frequency indicates the number of times a given predictor variable occurred in the 13 models with delta AIC <2.