

A HABITAT SUITABILITY MODEL FOR THE BIOCONTROL AGENT

MECINUS JANTHINIFORMIS IN IDAHO

by

Zachary Edward Nelson

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ABSTRACT

Since the introduction of Dalmatian toadflax (*Linaria dalmatica* (L.) Miller) to North America in the late 1800s, it has become a costly invasive species throughout the western United States. To manage the ecological as well as economic impacts from Dalmatian toadflax invasion, a biological control program was initiated. An important biological control agent for Dalmatian toadflax, the stem-mining weevil *Mecinus janthiniformis* Tosevski & Caldara, was released in Canada in 1991 and the U.S. in 1996. To determine the effectiveness of biological control agents like *M. janthiniformis*, the Idaho State Department of Agriculture created a standardized impact monitoring protocol (SIMP). The SIMP allows land managers to take a more active role in monitoring the progress of *M. janthiniformis*. Therefore, I used the SIMP data collected from land managers to determine the effectiveness of *M. janthiniformis* at 31 sites throughout Idaho. All but one of the sites had reductions in Dalmatian toadflax, 24 of which had statistically significant reductions ($P > 0.05$). Sites that had effective reductions in Dalmatian toadflax densities were deemed suitable habitats for *M. janthiniformis*. I used environmental conditions (elevation, temperature, and aspect) at sites with suitable habitats and data from literature reviews to create a habitat suitability model for Idaho. The habitat suitability model can be used to measure the effectiveness of the biological control program in Idaho. I overlaid biological control release sites on the habitat suitability model to determine the habitat quality at the release sites. A total of 206 releases of *M. janthiniformis* were found, and from the results of the habitat suitability model, I deemed that 70 releases were in areas where the weevil is unlikely to establish. Many of these releases were clumped together, indicating multiple failed establishments. These results show that the creation of habitat suitability models can be an effective means to measure the effectiveness of biological control programs and provide information for implementing future programs.

INTRODUCTION

As new technologies improve the efficiency of international commerce and travel, the spread of invasive species becomes more challenging to contain. The world is becoming more connected, bringing the potential for species to travel farther beyond their native range than ever before. Once established, these invasions can spread rapidly and cause considerable economic and ecological damage. Biological invasions have cost the North American economy at least \$1.2 trillion between 1960 and 2020, with costs climbing over the recent decades from an average of \$2 billion per year in the 1960s to over \$21 billion per year in the 2010s (Fantle-Lepczyk et al., 2022). Of that \$1.2 trillion, over two-thirds (\$896.2 billion) resulted from resource damage and losses, with \$190.45 billion resulting from invasive plant species (Fantle-Lepczyk et al., 2020). Resource damage and losses caused by invasive plant species are due to reductions in crop yield and forage quality for livestock (Radosevich et al., 2007). One such invader found in 30 states and four Canadian provinces is Dalmatian toadflax (*Linaria dalmatica* (L.) Miller) (Figure 1).

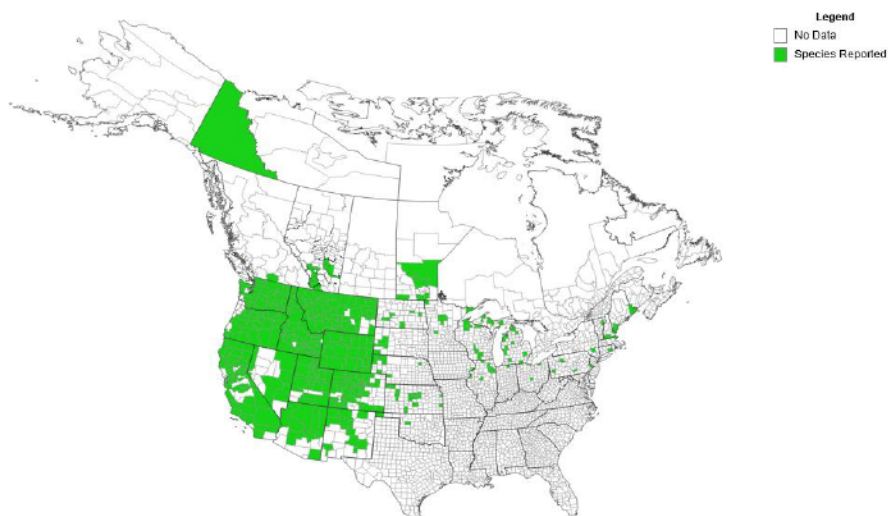


Figure 1. Confirmed sightings of Dalmatian toadflax in counties throughout Canada and the United States (EDDMapS 2023).

Initially found in southeastern Europe near the Mediterranean, *L. dalmatica* was introduced to North America in the late 1800s as an ornamental (Vujnovic & Wein, 1997). Since its introduction, *L. dalmatica* has spread rapidly throughout the Western United States, where it is a noxious weed in 14 states (Sing et al., 2016). A noxious weed is “any plant or plant product that can directly or indirectly injure or cause damage to crops, livestock, poultry, or other interests of agriculture, irrigation, navigation, the natural resources of the United States, the public health, or the environment” (USDA, 2023).

Not to be confused with yellow toadflax (*Linaria vulgaris* (L.) Mill), a similar invasive species native to Eurasia that was introduced to North America as an ornamental in the late 1600s (Lajeunesse, 1999). Although the *Linaria* species share similar snapdragon-shaped flowers, their leaves can easily distinguish the two species (Vujnovic & Wein, 1997). The leaves of *L. vulgaris* are narrow (3 to 6 mm wide), linear (2.5 to 5 cm long), and somewhat pointed at the end (Lajeunesse, 1999). Although the two species are distinct, hybrids can occur in areas where both species are present. Hybrid toadflax (*Linaria vulgaris* x *L. dalmatica*) plants present traits intermediate to the two parent species, *L. vulgaris* and *L. dalmatica*, depending on their genetic contributions (Ward et al., 2009).

Linaria dalmatica is a short-lived (three–five years) invasive perennial forb that can produce multiple stems, each reaching from 0.3 to 1.2 m in height (Alex, 1962). Plants produce one to 20 erect leafy stems with a waxy appearance (Lajeunesse, 1999) and nonflowering prostrate stems (Robocker et al., 1972). Leaves are heart-shaped, two and a half to eight cm long, one to two cm wide, and alternate up the stem (Lajeunesse, 1999). Flowers are snapdragon-shaped and bright yellow with orange centers that grow from the upper leaf nodes (Lajeunesse, 1999). Each fertilized flower can produce 60 to 300 seeds, and a mature plant with 10 to 15

reproductive stems can produce up to 400,000 to 500,000 seeds annually under the right conditions (Alex, 1962; Robocker, 1970). *Linaria dalmatica* develops large, well-developed taproots that can reach depths of three meters. Below-ground stems (rhizomes) produce lateral branches with vegetative buds extending from the parent plant to produce new plants (Robocker, 1974). Severed rhizomes as small as one centimeter can root and emerge as stems to produce new plants (Sing et al., 2016).

Linaria dalmatica seeds germinate primarily in the spring, from mid-March to early May, depending on site conditions, but they can also occur in the fall. Germination rates can be as high as 75% with viability of at least ten years (Robocker, 1970). In the first growing season, the plants produce two to five erect flowering stems and nonflowering prostrate stems. These prostrate stems remain green throughout the winter and are an essential carbohydrate storage source for the following growing season (Robocker, 1974; Sing et al., 2016). Flowering generally occurs in June but can happen as early as May. *Linaria dalmatica* is a self-sterile, insect-pollinated species (Vujnovic & Wein, 1997) by many different species of bumblebees and halictid bees (Sheley, 1994). Seed production begins in the summer and into the fall, where they gradually begin to dehisce and disperse via wildlife (grazing ungulates), surface runoff, and wind (Robocker, 1970). Dispersal distance by wind is minimal, as 80 to 90% of the seed produced falls within 0.8 m of the mother plant (Nadeau & King, 1991).

The morphology and lack of natural enemies significantly factor into *L. dalmatica*'s invasiveness and dominance in its introduced range. The enemy release hypothesis proposes that the success of non-native species is related to the lack of enemies in their introduced range compared to where they originated from in their native range (Meijer et al., 2016). Therefore, *L. dalmatica* is less susceptible to herbivory by animals or insects in their introduced range of North

America compared to their native range of Southeastern Europe. The characteristics of *L. dalmatica* responsible for its invasiveness include the previously mentioned rhizomatous root system, high seed production rate, and the ability to produce allelochemicals (De Clerck-Floate & Turner, 2013).

The allelochemicals of consequence produced by *L. dalmatica* are iridoid glycosides that defend the plant from infections but also act as a deterrent for generalist herbivores due to their bitter taste (Biere et al., 2004; Beninger et al., 2007; Jamieson & Bowers, 2010; Matveeva et al., 2015). Iridoid glycosides are a group of cyclopentanoid monoterpene-derived compounds found in approximately 50 plant families (El-Naggar & Beal, 1980; Jamieson & Bowers, 2010). The two major iridoid glycosides produced by *L. dalmatica* are antirrhinoside and linarioside (Jamieson & Bowers, 2010). Leaves containing antirrhinoside deterred the generalist herbivore *Lymantria dispar* (spongy moth), and moth growth was negatively impacted when fed a diet containing concentrations lower than those found in leaves (Beninger et al., 2008). Production of these iridoid glycosides is at its highest in areas with lower precipitation rates (Jamieson et al., 2013), like those found in the western United States, where *L. dalmatica* thrives (EDDMapS, 2023).

The dual modes of reproduction, lack of natural enemies, and deterrent of generalist herbivores allow *L. dalmatica* to invade and outcompete native vegetation. The proliferation of *L. dalmatica* ultimately reduces biodiversity and creates monocultures as the native plant populations get displaced. Losing native vegetation reduces the forage quality for wildlife and livestock (Sheley, 1994). While some animals will feed on *L. dalmatica*, it is not considered a favored or necessary component of any wildlife species' diet (Sing and Peterson 2011). One way

to reduce the impact of *L. dalmatica* is to use living organisms (biological control) to reduce the weed's competitive advantage over native vegetation.

Biological Control

Biological control (biocontrol) uses natural enemies (agents) to reduce pest populations (USDA, 2023). Biocontrol agents can be vertebrates, invertebrates, and microorganisms. Successful agents have a narrow host range, adapt to different climates, synchronization with the target pest's lifecycle, produce large amounts of offspring, effectively locate their host, and survive at low host density (Murdoch et al., 1985). There are three general methods of biological control: promoting the survival of existing natural enemies (conservation), collection of natural enemies from their origin to establish in a new area where their host has been introduced (classical biological control), and periodic release of large numbers of mass-reared natural enemies (augmentation) (Chidawanyika et al., 2012). Careful selection and testing of the biocontrol agent are performed before introduction to the novel habitat to ensure there will be no impact on any native species. An international code of best practices for classical biological control of weeds was developed to improve the efficacy of biocontrol and reduce its potential negative impacts (Figure 2).

Different biocontrol agents attack target pest plants in different ways, including targeting the plants' roots, stems, foliage, seeds, or flowers. The different modes of attack have varying levels of effectiveness depending on the morphology and phenology of the target plant. Root- and crown-feeding agents are generally more effective against perennial rhizomatous plants, while flower- and seed-feeding agents are more effective against annual and biennial plants that are primarily spread by seed (Sing et al., 2016). Because the agents rely on the target pest plants

for nutrition and reproduction, biocontrol is unlikely to eradicate the pest plant. However, when coupled with other stressors, the target plant's ability to compete with native vegetation is reduced.

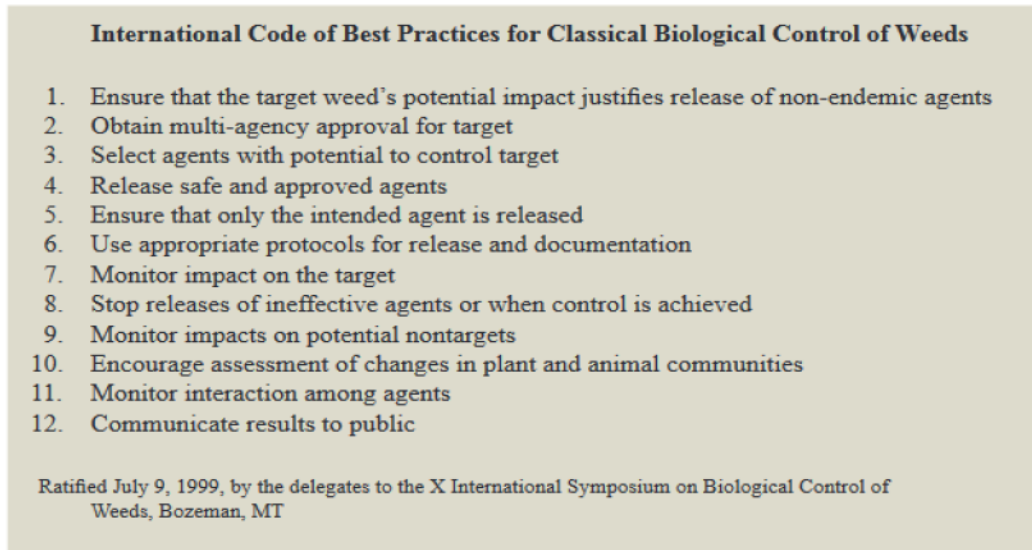


Figure 2. International code of best practices for classical biological control of weeds developed by the delegates at the Tenth International Symposium for Biological Control of Weeds (Pg. 5 in Sing et al., 2016).

Biocontrol for *L. dalmatica* in North America started in the late 1960s, and since then, five agents have been tested and released (De Clerck-Floate & Turner, 2013). These agents are the defoliating moth (*Calophasia lunula* Hufnagel, 1766), Toadflax flower beetle (*Brachypterolus pulicarius* Linnaeus, 1758), seed capsule-feeding weevil (*Rhinusa antirrhini* Paykull, 1800), Root-mining cosmet moth (*Eteobalea intermediella* Riedl, 1966), and Dalmatian toadflax stem-mining weevil (*Mecinus janthiniformis* Tosevski & Caldara, 2011). Three out of five of the agents released have established on *L. dalmatica*: *C. lunula*, *R. antirrhini*, and *M. janthiniformis* (Gassmann & Parker, 2016). Neither *E. intermediella* nor *B. pulicarius* has established on *L. dalmatica* due to the cryptic nature of *E. intermediella* and the preference of *B. pulicarius* for *L. vulgaris* (MacKinnon et al., 2005). While *C. lunula* and *R. antirrhini*

successfully established on *L. dalmatica*, their modes of injury are defoliation and seed feeding, respectively, which is less effective against the perennial rhizomatous *L. dalmatica* (Jacobs & Sing, 2006). Because of stem-mining in the larval stage and defoliation in the adult stage, the most successful of these agents at reducing populations of *L. dalmatica* is *M. janthiniformis* (Gassmann & Parker, 2016).

Mecinus janthiniformis is a univoltine weevil native to Eurasia introduced to North America in 1991 in Canada by the Canadian Food Inspection Agency (McClay & Hughes, 2007; Tosevski et al., 2011). Approval for release in the United States came in 1996 by the U.S. Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS). *Mecinus janthiniformis* prefers habitats consisting of open areas with hot, dry conditions like rangelands, pastures, montane meadows, and open arid forests (Tosevski et al., 2011; Sing et al., 2016).

Mecinus janthiniformis was initially thought to be the yellow toadflax stem-mining weevil *Mecinus janthinus* Germar, 1821; however, *M. janthiniformis* was identified as a distinct species through DNA analyses (Tosevski et al., 2011). While very similar in appearance, *M. janthiniformis* adults are nearly twice as big as *M. janthinus* adults (3.2 – 6.0 mm vs 2.4 – 3.4 mm long) (Tosevski et al., 2011) (Figure 3). Also, *M. janthiniformis* is a metallic black with hues of blue. The rostrum is long and curved in males (~0.80 – 0.88 times as long as pronotum length)



Figure 18. Comparison of size of a) *Mecinus janthinus* and b) *Mecinus janthiniformis* (Tosevski et al., 2011).

and longer and more curved in females ($\sim 1.03 - 1.09$ times as long as pronotum length). Males have strongly toothed front femurs not found on females (Carney et al., 2004).

Adults emerge in early spring from *L. dalmatica* stems established in the previous growing season and feed on the foliage from the new growing season (Figure 4). Emergence times can vary depending on site characteristics such as elevation, latitude, aspect, and snow cover (Sing et al., 2016). Foliar feeding produces noticeable shot-hole shapes in the leaves, potentially reducing the photosynthetic capacity of the leaves and possibly leading to plant deformity. Mating and egg-laying begins immediately following emergence in the spring and can last till mid-July. Females chew cavities into the upper portion of the main stem and lay a single egg in each, covering the eggs with chewed plant tissue.



Figure 34. Adult *M. janthiniformis* overwintering in the stem of dalmatian toadflax (Smith et al. 2021).

Egg laying occurs daily at one egg per day, with females able to lay as many as 45 eggs in a lifetime (Sing et al., 2016; Tosevski & Caldara, 2020). Eggs hatch into larvae in six to seven days under laboratory conditions and feed on tissue in the stems, creating tunnels. The larvae go through three instars and develop into pupae in 23 to 40 days. Adults emerge from the pupae in 27 to 29 days but remain in the pupal cell, where they overwinter until they emerge from the

stem the following spring (Jeanneret & Schroeder, 1992) (Figure 5). Mortality rates during the overwintering stage can reach 75 to 100% in areas where the temperature drops below -28 °C (-18.5 °F) (De Clerck-Floate & Miller, 2002).

The success of *M. janthiniformis* as a biocontrol agent is from the damage to the stems of *L. dalmatica* during the larval stage, which impairs the plant's ability to transport water and nutrients (Saner et al., 1994). A sufficiently high density of *M. janthiniformis* can create a

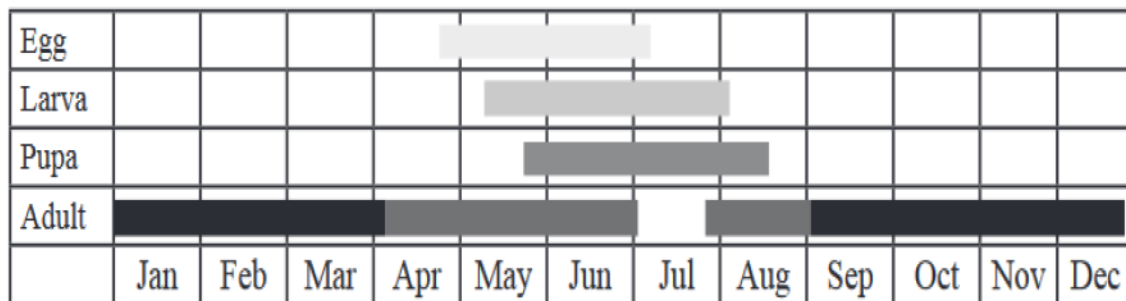


Figure 50. Life cycle of *M. janthiniformis*. Bars indicate the approximate amount of time spent at each life stage. Black bars represent the overwintering period (Figure 36 in Sing et al., 2016).

nutrient deficiency, causing reductions in stem and root biomass (Schat et al., 2011). *Mecinus janthiniformis* are strong fliers that can quickly disperse through infested areas, making them highly mobile agents (Sing et al., 2016). Park et al. 2014 found that *M. janthiniformis* could move up to 60 km from release sites independent of human facilitation.

HABITAT SUITABILITY MODEL

A habitat suitability model is an operational application of the ecological niche, using environmental variables to predict the presence or absence of a species throughout a study area (Hirzel & Le Lay, 2008). An ecological niche is defined in several ways. Grinnell (1917) posited

that the ecological niche of a species was the ecological conditions within which a species can maintain populations without immigration. Hutchinson (1959) distinguished the fundamental niche as the range of theoretical possibilities for the species' habitat and the realized niche concerning habitats the species occupies. The ecological niche theory links the fitness of the individuals in a species to conditions in their environment, allowing for the quantifiable classification of those conditions in relation to their effect on fitness. Habitat suitability models use the environmental conditions that most directly limit species distribution.

There are many different methods of creating habitat suitability models depending on the data available, the species observed, the study's goal, and the study's location. These methods can fit broadly into two categories: literature review and empirical statistical methods. Literature review methods use current studies to assign a value to environmental factors based on the importance that factor has on species distribution. The values for all the environmental factors selected are combined to create a habitat suitability model, with a value created for each pixel representing the suitability of the location. This method does not require field data, making it useful for locations where accurate presence or absence data for species are unknown or lacking. Empirical statistical methods use field data to determine presence and absence locations of the target species. Statistical techniques then use the environmental factors at the determined presence and absence locations to predict the species distribution in the study area. This method can produce more accurate results but requires precise field data, which can be challenging to acquire.

Once developed, there are many uses for habitat suitability models. Trethowan et al. (2011) used habitat suitability models to show areas where habitats may overlap between the invasive pompom weed (*Campuloclinium macrocephalum* Less.) and two potential biocontrol

agents, a flower-feeding lepidopteran (*Cochylis campuloclinium* Brown, 2006) and stem-galling thrips (*Liothrips tractabilis* Mound & Pereyra) in southern Africa. Augustinus et al. (2020) used field and laboratory experiments to determine climate-dependent parameters most relevant to the proliferation of the North American leaf beetle (*Ophraella communa* LeSage, 1986), a potential biocontrol agent for common ragweed (*Ambrosia artemisiifolia* L.) to project population ranges across Europe. For this study, I use the created habitat suitability map to monitor how many releases of *M. janthiniformis* have occurred in locations with suitable habitats in the state of Idaho.

METHODS

Standardized Impact Monitoring Protocol (SIMP)

I collected SIMP data on 05/30/2023 from iBiocontrol.org, a database for SIMP data collected from various agencies and landowners. The SIMP data were filtered for *M. janthiniformis* sites throughout Idaho with at least five years' worth of data. Six sites were removed due to evidence of herbicide application, resulting in 31 sites to determine the effectiveness of *M. janthiniformis* in reducing the percentage cover of *L. dalmatica*.

I grouped the 31 sites based on the number of years monitored (5- to 12-year-long studies between 2007 and 2018) and recorded the average percentage cover of *L. dalmatica* for each year within the groups. I calculated the linear regression for each group to determine the percentage cover at all 31 sites. Linear regression models and Spearman's rank correlations were collected for each site individually to determine the strength of the relationship between the time since release of *M. janthiniformis* and the percentage cover of *L. dalmatica* at those sites. Sites with significant regression models (p-value < 0.05) and R² values that show a good fit (between

0.50 and 0.99) were deemed suitable habitat for *M. janthiniformis*. Conditions at these sites from the SIMP data are collected and used in implementing the habitat suitability model. Non-significant sites with low R^2 values indicate sites with less suitability. Site conditions included elevation, average air temperature, average precipitation, and days between frosts.

Developed by the Idaho State Department of Agriculture, in conjunction with the University of Idaho, Nez Perce Biocontrol Center, and federal land management agencies, SIMP is a way for land managers to take a more active role in monitoring the progress of biocontrol agents (iBiocontrol, 05/30/2023). SIMP involves using a randomly placed permanent 20-m long transect in an area infested with the target weed. To start, a post is placed at the start of the transect, followed by permanent markers every two meters along the 20-m transect for a total of 10 markers. A 25 x 50 cm Daubenmire frame made from PVC or rebar is placed parallel to the transect line with the 50-cm side along the transect. The permanent marker is in the upper left-hand corner of the Daubenmire frame (Figure 6). Data collection involves measuring the percentage cover located in each Daubenmire frame. Categories for percentage cover include the percentage of the target weed, other weeds,

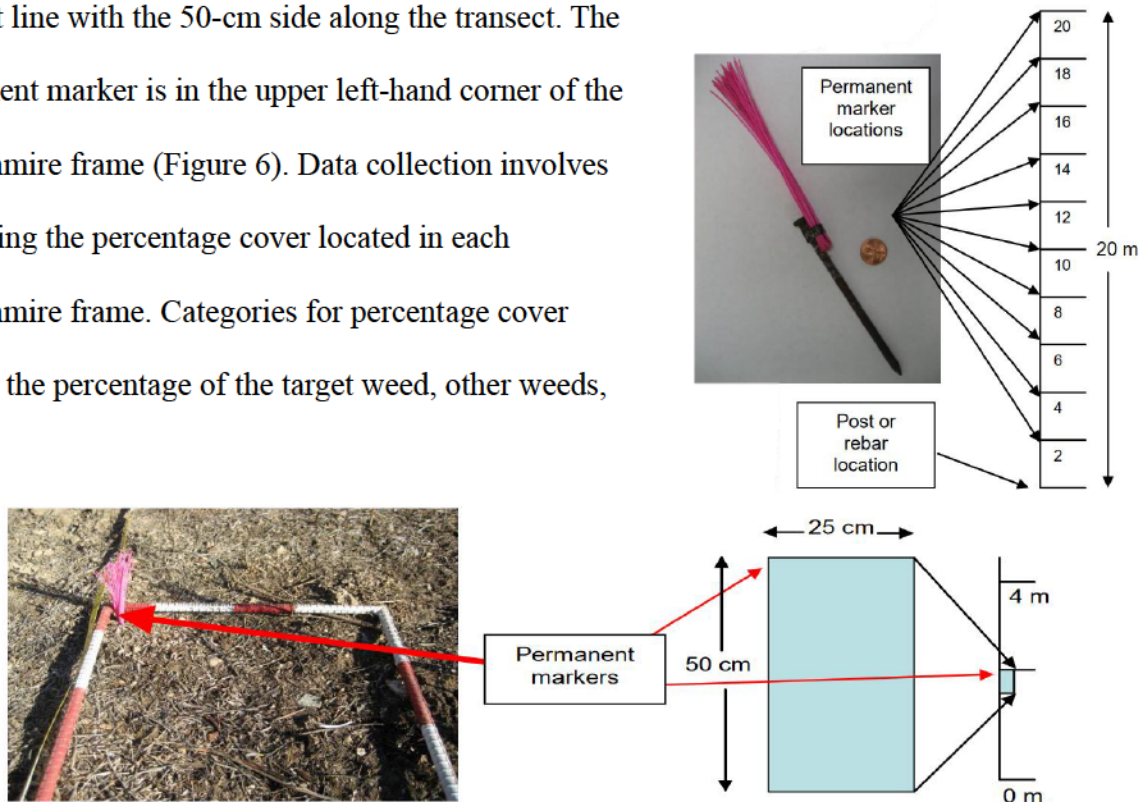


Figure 51. Standardized impact monitoring protocol (SIMP) setup (Figure 3 & 4 in iBiocontrol.org).

forbs, grasses, bare ground, litter, and moss. Additional important information required is the observer's name, date, landowner, site name, target weed, biocontrol agent, latitude, longitude, insect stage, and whether the site is permanent. Target weed size and density are recorded by counting the number of stems of the target weed in each frame and the height of the tallest stem. Sweeps of the area are performed to obtain insect counts for the biocontrol agent. A sweep is a three-minute timed count of the area performed six times, recording the number of biocontrol agents counted.

Data Sources

The habitat suitability model consisted of land cover, minimum temperature, average temperature, elevation, and aspect data. Land cover data were acquired from the Commission for Environmental Cooperation (CEC) as part of the North American Land Change Monitoring System (NALCMS) (Commission for Environmental Cooperation (CEC), 2023). The main inputs for image classification were from the 30-m spatial resolution Landsat 8 collection 2 level 1 data for 2015 consisting of landcover types for the state of Idaho (Figure 7).

Elevation data were acquired from the National Elevation Dataset (NED) digital elevation model (DEM) developed by the U.S. Geological Survey (U.S. Geological Survey, 2000). Data collection contains 1/3 arc-second (~10 m) resolution digital elevation datasets for the state of Idaho. The DEM dataset was used to create an aspect raster using the GDAL tool Aspect in QGIS. This aspect raster contains information on the direction in which the slope of the terrain is facing. Raster data contain points from 0 – 359 depending on the direction the slope is facing. An aspect of zero means that the slope of that terrain is facing north, 90 is facing east, 180 is facing south, and 270 is facing west. Temperature datasets for 2012 were acquired from

the PRISM Climate Group at Oregon State University; 2012 was chosen because sites were monitored sometime between 2007 and 2018. Data acquired included minimum temperatures in January and mean temperature for the month of July.

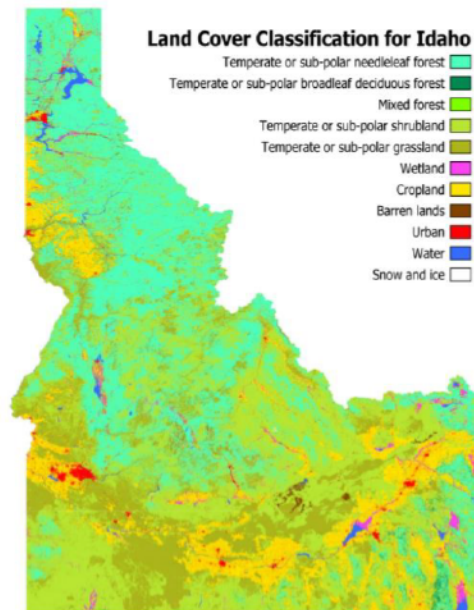


Figure 52. Idaho land cover classification scheme from the North American Land Change Monitoring System (NALCMS) (Commission for Environmental Cooperation (CEC), 2023).

Model Methodology

The habitat suitability model created in my study displays the suitable habitat for *M. janthiniformis* in the state of Idaho. The method selected for this study was the literature review approach that uses available studies and land cover data to create a habitat suitability index (Muhammed et al., 2022). A habitat suitability index is an index that gives numerical values to habitat attributes to assess the habitats' ability to support a species (EPA, 2023). I chose this method because *M. janthiniformis* is an intentionally introduced species in Idaho with environmental conditions different from the native range of southeastern Europe. As such, any

presence or absence data may be biased to locations based on release sites that may or may not use accurate information. Because releases have occurred from different agencies and landowners, it is impossible to know the basis behind all the releases. Thus, whether the species will establish in those locations is unknown and cannot be used to develop a habitat suitability model. Areas in the study area with accurate presence data were determined using data collected from SIMP sites. However, there was not a large enough sample size (24) to represent the entire study area, so models that used the conditions at these sites would not be representative of the whole study area.

To justify the selection of the literature review method, I created another habitat suitability model using a method that requires presence data. The method I used was maximum entropy modeling (MaxEnt), which uses georeferenced species occurrence locations and datasets containing environmental factors to predict suitable conditions for the species throughout the study area. The MaxEnt method was selected because the model only requires presence data and not absence data. This is important because determining true absence can be difficult in an uncontrolled setting (Pinti et al., 2022). I used the latitude and longitudes of 24 SIMP sites for the occurrence locations of *M. janthiniformis* and the same environmental datasets used in developing the literature review model. Results from the literature review and MaxEnt models were compared to determine which method is better for predicting suitable habitat for *M. janthiniformis*.

Data Analysis

Statistical analysis was performed using R for Windows version 4.3.1. Linear regression models were calculated for each site with the average *L. dalmatica* cover per year as the

dependent variable and time since release in years of *M. janthiniformis* as the independent variable. A line of best fit was created to show the magnitude and direction (β_1) of the trend and the coefficient of determination (R^2). The sites were then listed in order based on their elevations with their β_1 and R^2 values to determine if any trends developed as the elevation of the sites increased. Spearman correlations were run between the average percentage cover per year of *L. dalmatica* and the time since release in years of *M. janthiniformis*. The Spearman correlation measures the strength and direction of association between the two variables.

The habitat suitability model was created using QGIS version 3.32.3 'Lima.' Using the raster calculator in QGIS, a habitat suitability index for temperature, elevation, aspect, and land cover was completed (Figure 8). Again, these indices were combined using the raster calculator

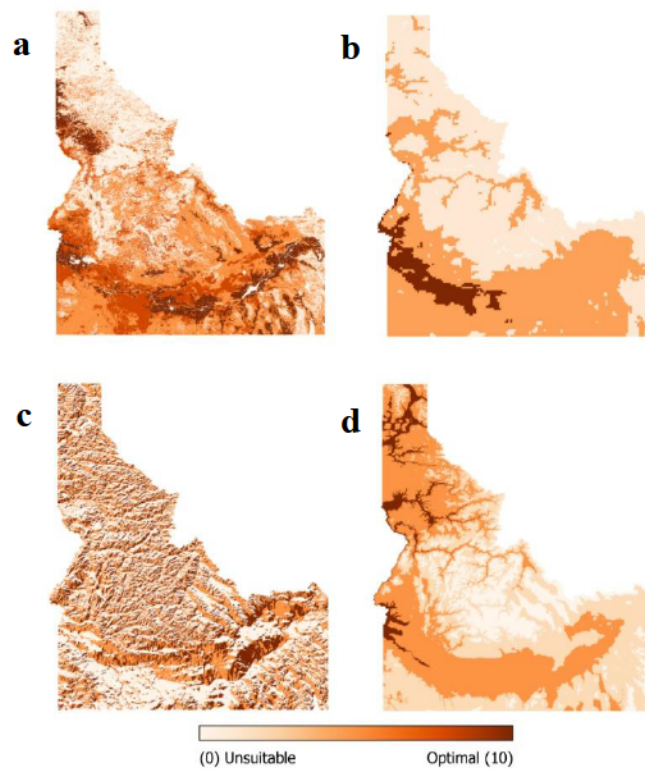


Figure 53. Habitat suitability indices for a) landcover, b) temperature, c) aspect, and d) elevation.

to create the final habitat suitability model. Latitude and longitudes of the SIMP sites were collected from iBiocontrol.org, and their points were added to the habitat suitability model. The locations' suitability level from the habitat suitability model were compared to the results of the linear regression models to gauge the model's accuracy. The latitudes and longitudes of all the biocontrol release sites for *M. janthiniformis* were also collected from iBiocontrol.org and added to the habitat suitability model to determine the effectiveness of the releases.

RESULTS

Individual linear regression models of the 31 sites found that 24 sites show statistically significant reductions in the percentage cover of *L. dalmatica* as a function of years after the release of *M. janthiniformis* (Table 1). Only Lake Creek, out of the sites included, shows an increase in *L. dalmatica* percentage. Median values of rho (ρ) and the coefficient of determination (R^2) for the 24 SIMP sites that show significance were 0.77 and 0.58, respectively.

A review of the literature has shown that the environmental variables necessary to predict the occurrence of *M. janthiniformis* are mean temperature during the hottest month, minimum temperature, elevation, aspect, and land cover. Habitat suitability values for the minimum temperature dataset were based on De Clerck-Floate and Miller (2002), who determined that *M. janthiniformis* experiences high mortality rates at -28 °C. Therefore, a value of zero was given to areas of Idaho that reached -28 °C or below in the month of January 2012. The values for the dataset for the mean temperature for July 2012 were based on Tosevski & Caldara (2020) and McClay & Hughes (2007), in which they determined larval development rates increased with temperature. Median oviposition to adult development times ranged from 45 days at 30 °C to 116 days at 15 °C. The increase in development times plateaued around 30 °C and started decreasing

at higher temperatures. Based on these findings, a value of 10 was placed on areas that averaged between 25 °C and 30 °C. Areas that averaged between 20 °C and 25 °C received a value of eight

*Table 1. Results of the linear regression models and Spearman correlation for the percentage cover of *L. dalmatica* as explained by the years since release of *M. janthiniformis*. Showing the number of years monitored at each site with its elevation.*

Site	Elevation (m)	Years	Linear Regression			Spearman Correlation	
			β_1	P	R ²	ρ	P
<i>Cove Ranch</i>	1959	10	-0.98 ± 0.32	0.017	0.53	-0.77	0.009
<i>Slaughterhouse</i>	1917	9	-1.04 ± 0.43	0.045	0.46	-0.63	0.069
<i>Baldy Palisades</i>	1905	12	-0.95 ± 0.14	<0.001	0.82	-0.94	<0.001
<i>Bear Lake</i>	1863	9	-0.71 ± 0.39	0.392	0.32	-0.54	0.137
<i>Patterson</i>	1839	5	-1.20 ± 0.69	0.182	0.50	-0.71	0.182
<i>Lake Creek</i>	1812	12	0.06 ± 0.12	0.585	0.03	0.17	0.591
<i>Caribou</i>	1653	11	-1.49 ± 0.43	0.007	0.58	-0.67	0.024
<i>Rick Brown</i>	1631	6	-1.00 ± 0.59	0.165	0.42	-0.46	0.354
<i>Ten Ax</i>	1396	12	-0.69 ± 0.17	0.002	0.62	-0.84	0.001
<i>Snake River Breaks</i>	1174	12	-0.59 ± 0.18	0.009	0.51	-0.76	0.004
<i>Helispot</i>	1151	12	-0.09 ± 0.08	0.266	0.12	-0.24	0.444
<i>Huckleberry</i>	1151	11	-0.49 ± 0.13	0.005	0.60	-0.72	0.012
<i>DOTY</i>	1151	12	-0.58 ± 0.18	0.009	0.51	-0.77	0.004
<i>Center Canyon 3</i>	1128	5	-2.30 ± 0.75	0.055	0.76	-0.89	0.041
<i>Rice Creek</i>	1128	11	-0.95 ± 0.37	0.031	0.42	-0.66	0.028
<i>Cold Springs</i>	991	11	-0.95 ± 0.28	0.008	0.56	-0.75	0.007
<i>Center Canyon 1</i>	991	5	-6.90 ± 2.43	0.065	0.73	-0.90	0.083
<i>Center Canyon 2</i>	991	5	-3.65 ± 0.66	0.012	0.91	-0.97	0.005
<i>Pine Creek</i>	985	11	-0.36 ± 0.12	0.126	0.52	-0.64	0.034
<i>Port Hill</i>	853	12	-0.68 ± 0.20	0.007	0.53	-0.76	0.004
<i>Cuprum DT</i>	811	10	-1.09 ± 0.28	0.005	0.65	-0.85	0.002
<i>Idaho Hill Transfer</i>	762	11	-1.01 ± 0.37	0.024	0.45	-0.58	0.063
<i>Slate Creek</i>	747	5	-2.15 ± 0.53	0.026	0.85	-0.97	0.005
<i>Little Salmon River 1</i>	732	5	-1.80 ± 0.43	0.025	0.85	-0.87	0.054
<i>Little Salmon River 2</i>	732	5	-3.60 ± 0.99	0.036	0.82	-0.97	0.005
<i>Lone Mountain</i>	732	12	-0.55 ± 0.15	0.004	0.57	-0.89	<0.001
<i>Farragut State Park</i>	702	11	-0.31 ± 0.09	0.009	0.55	-0.76	0.007
<i>Moyie Store</i>	701	8	-0.32 ± 0.11	0.024	0.60	-0.70	0.052
<i>Pine Bar</i>	694	10	-0.67 ± 0.16	0.003	0.68	-0.86	0.001
<i>Squaw Creek</i>	404	5	-3.70 ± 0.87	0.024	0.86	-0.97	0.005
<i>Idaho Border</i>	296	12	-0.90 ± 0.24	0.004	0.58	-0.71	0.009

as these conditions are favorable. The value of five was assigned to areas averaging between 15 °C and 20 °C, and anything lower than 15 °C received a zero.

Elevation habitat suitability values were determined from analysis of linear regression models of the SIMP data and a study by Tosevski et al. (2011) that determined that *M. janthiniformis* can be found from low elevations up to 1500 m. While SIMP data show the successful establishment of the weevils at elevations above 1500 m, there seem to be slight reductions in statistical significance with elevations above 900 m and again with elevations above 1500 m (Table 1). This evidence suggests that elevations between 1500 and 2000 m are suitable but not optimal and thus are valued less than elevations below 1500 m. The data also show an increase in suitability at elevations below 900 m. Due to these findings, a value of 10 was given to elevations below 900 m, eight was assigned to elevations from 901 to 1500 m, and five was assigned to elevations from 1501 to 2000 m.

Because *M. janthiniformis* prefers a hot and dry climate, a south-facing aspect will be more suitable (McClay & Hughes, 2007). The weevil's food source and host for reproduction, *L. dalmatica*, sprouts faster and re-establishes faster after a disturbance on southern slopes (Ross, n.d.; Lajeunesse, 1999; Blumenthal et al., 2012). The abundance of food and sun provides an optimal habitat for *M. janthiniformis*. For the aspect raster, any aspect between 202.5 and 247.5 degrees was valued highly and thus received a value of 10. Aspects between 112.5 and 202.5 degrees are suitable habitats and received a value of eight. Aspects between 247.5 and 337.5 degrees received a value of five, while aspects greater than 337.5 and less than 112.5 received a low value of two because a Northeast aspect receives the least amount of sunlight.

For the land cover dataset, Sing et al. (2016) and Tosevski et al. (2011) state that *M. janthiniformis* prefer pastures, rangeland, montane meadows, and arid forest. Tosevski and

Caldara (2020) also state that *M. janthiniformis* prefers grassland or open forested areas with hot, dry conditions. Classification schemes were ranked as bare ground, cropland, temperate or sub-polar grassland, and temperate or sub-polar shrubland from most likely to least likely. The remaining classification schemes received a value of zero as it is doubtful that *M. janthiniformis* would be found in those habitats.

The values created from the literature review model show that 46.8% of the pixels in the study area have a value of five or more, which indicates a suitable habitat, and optimal habitat (7.5 or greater) was 8.2% of the study area (Figure 9a). The mean of these values was 4.6, with a standard deviation of 1.9. There was no information on the percentage of pixel values for the MaxEnt model; however, it is clear that suitable habitat is much lower in comparison (Figure 9b).

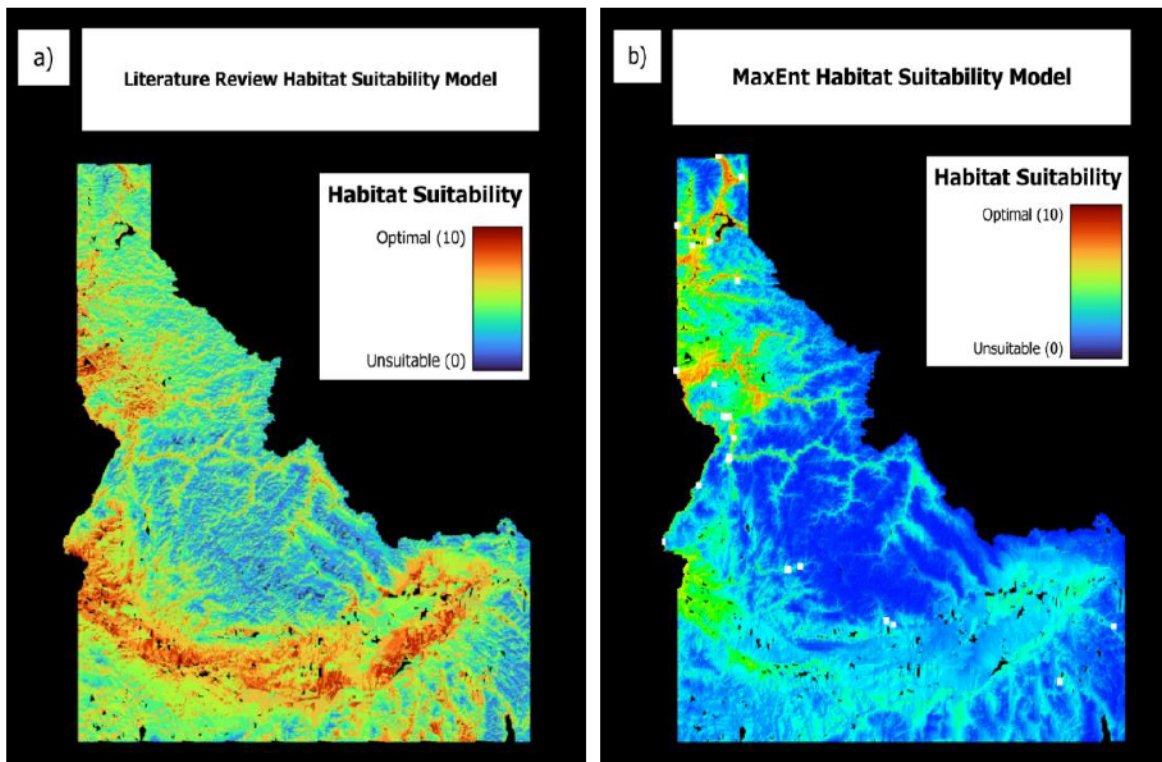


Figure 54. Comparison of a) literature review model and b) MaxEnt model. White dots on MaxEnt model indicate locations used for presence data.

Results from the MaxEnt model suggest that elevation is the most important in determining species distribution out of the environmental factors used to create the model. Elevation has a permutation importance of 77.6%, suggesting that the model depends heavily on that variable. Permutation importance is determined by randomly permuting the values of the variable at the presence locations and measuring the resulting decrease in training area under the curve. The environmental variable with the next highest permutation importance is average temperature, with 11.7%. These results are mirrored in the jackknife test, which shows that elevation has the highest gain and largest decrease when omitted, suggesting that elevation provides the most useful information and information not present in other variables (Figure 10).



Figure 55. Results from Jackknife test of variable importance. Dark blue indicates training gain when variable is used in isolation. Light blue indicates the training gain when the variable is omitted. Red is the total training gain from all variables. (MaxEnt version 3.4.1)

Results from the linear regression models created from the SIMP data validate the literature review habitat suitability model. Of the regression models for the 31 sites, 24 correctly matched values from the habitat suitability model (Figure 11). A correct match means that significant models ($p < 0.05$) show a negative trend in *L. dalmatica* cover with site locations that represent an area on the model with a value of five or greater, and insignificant models ($p > 0.05$) represent areas on the model with a value less than five.

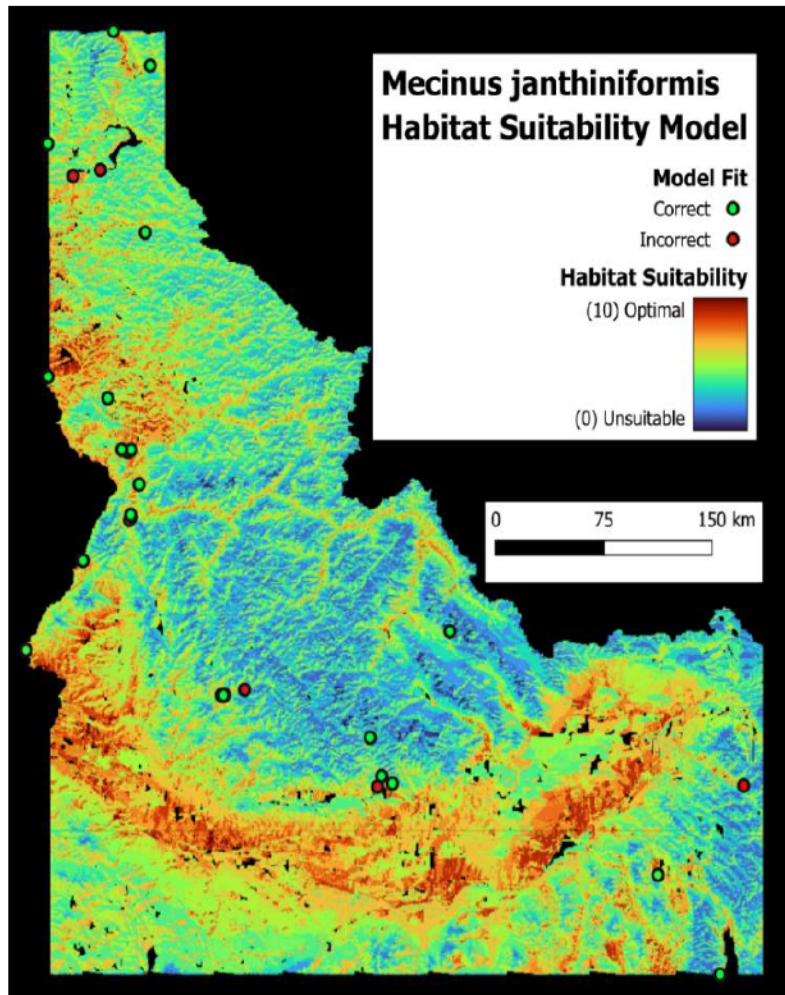


Figure 56. Habitat suitability model for *Mecinus janthiniformis* showing the SIMP sites used to determine the model fit. SIMP sites in green show locations where the data collected agrees with the habitat suitability model and locations in red where they do not.

The website iBiocontrol.org contains a total of 206 releases of *M. janthiniformis* in the state of Idaho (Figure 12). These releases have occurred throughout the state, with the majority on the west side near the border of Washington. Of these 206 releases, 70 fall in locations on the habitat suitability model that received values lower than five, indicating areas with less-than-optimal conditions for *M. janthiniformis*.

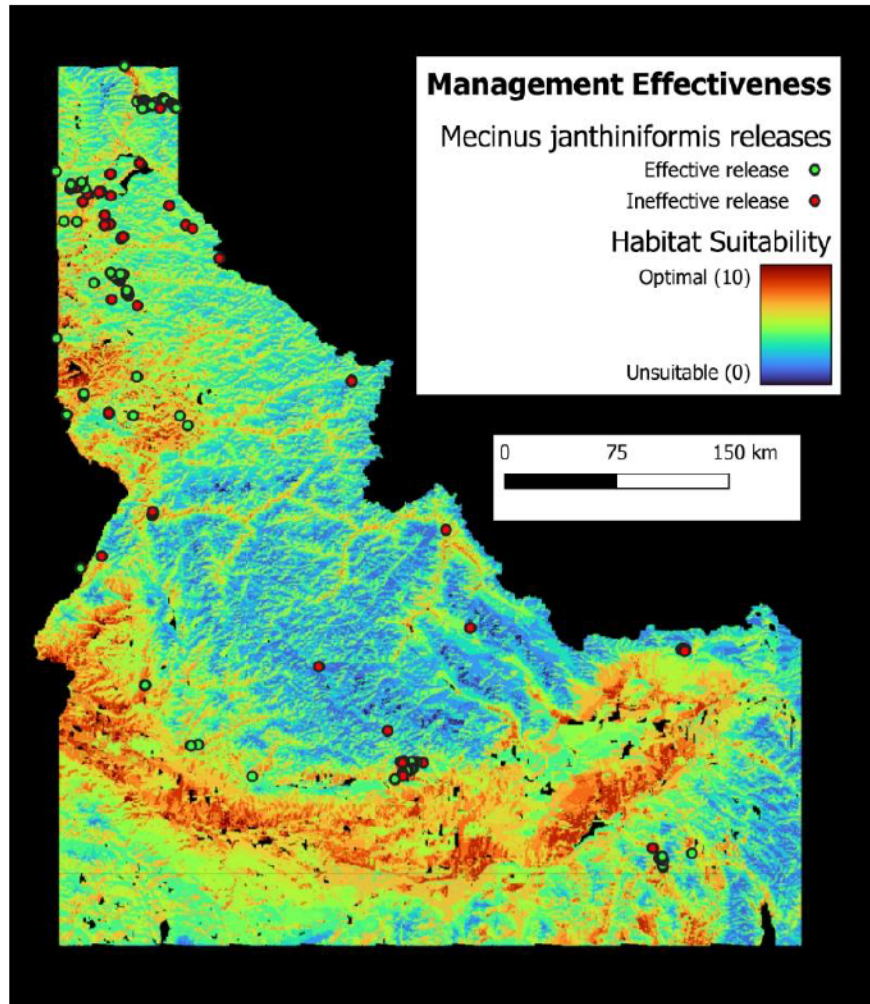


Figure 72. Biocontrol releases (206) in the state of Idaho overlaid on the habitat suitability model showing the releases on suitable habitat in green (136) and releases not on suitable habitat in red (70).

DISCUSSION

My analysis showed that *M. janthiniformis* successfully reduces populations of *L. dalmatica* in areas throughout Idaho. Of the 31 sites that met the necessary conditions, all but one show a reduction in cover for *L. dalmatica*. Of the 30 sites with negative trends, 24 (80%) show statistically significant trends. Due to a lack of a control group, causality cannot be determined; however, the results obtained in this study agree with the findings from Weed et al. (2018), in which they found that declines in *L. dalmatica* cover coincided with the time since

weevil release. Weed and Schwarzlander (2014) determined that a variable contributing to changes in *L. dalmatica* populations was the density of *M. janthiniformis*, in which higher weevil abundance led to reductions in *L. dalmatica* populations and lower weevil abundance was associated with increases in *L. dalmatica* populations. For *M. janthiniformis* to reproduce to levels necessary to reduce populations of *L. dalmatica*, the environmental conditions at those locations must be suitable habitats. These necessary environmental conditions are recorded in SIMP data. They can be used to assist in developing habitat suitability models that can aid in our management considerations for *L. dalmatica*.

I determined that there was not a large enough sample size of SIMP sites with suitable habitats for the use of presence only habitat suitability models. This was seen in the MaxEnt model, where the SIMP sites were used as presence locations for *M. janthiniformis*. From the MaxEnt model, you can see a decrease in suitable habitat when compared to the literature review model. I believe this is due to the small sample size (24) and the uneven distribution of the samples. The uneven distribution can cause an overestimation of the importance of some variables while underestimating others. The small sample size exacerbates the improper evaluation of the importance of the variables. This was evident in the large difference in permutation importance between elevation and the other variables. However, the SIMP sites could still be used to aid in determining the accuracy of the literature review habitat suitability model. I used SIMP data to determine model accuracy by overlaying the SIMP sites on the model and comparing the habitat suitability index score to the site's suitability. Of the 31 SIMP sites that met the requirements, 24 (77.4%) agreed with the habitat suitability model. This method of using SIMP data collected from land managers to verify the accuracy of the habitat

suitability model provides a less labor intensive and less time-consuming method of obtaining field data.

Biocontrol release locations for the study area were overlaid on the habitat suitability model to determine the effectiveness of the releases. Of the 206 releases, 70 fall outside of the suitable habitat for *M. janthiniformis*. These releases represent a lot of time and money spent that could be used elsewhere. Many of these releases in unsuitable habitats occur in clumps, indicating that multiple years of sampling were spent that could have been avoided had the land manager known that *M. janthiniformis* is unlikely to establish in those locations. Park et al. (2014) observed the biocontrol of *L. dalmatica* in Oregon, and from their results, they determined they may have over-applied weevils and that those resources could have been used elsewhere. They estimated the program's total cost to be \$142,350, which was still cost-effective compared to conventional control measures. However, the program could have been even more cost-effective if they had better-selected release sites.

While the cover percentage of *L. dalmatica* was low throughout the SIMP sites measured (Percent cover: max: 30, mean: 3.85, standard deviation: 4.41), these data reflect the cover found in the random and unbiased placement of the Daubenmire frames. Unbiased sampling is an attempt to show an accurate representation of the plant cover for the area; however, depending on the site, a single 20 m transect may not be a representative sample. Values for percentage cover are also subjective depending on the observer collecting the SIMP data, and the observers often change from year to year and site to site. Environmental conditions also vary from site to site and year to year, which may factor into changes in the percentage cover of *L. dalmatica* that are unrelated to the release of *M. janthiniformis*. However, the reduction in the cover of *L. dalmatica* at 30 of the 31 SIMP sites, despite the low starting cover, is a testament to the efficient

searchability of *M. janthiniformis*. Even the low percentage cover found at the SIMP sites has the potential to spread quickly, pushing out native species and reducing biodiversity and forage quality (Vujnovic & Wein, 1997).

In conclusion, *L. dalmatica* is an aggressive invader able to take over habitats with its unique reproductive characteristics and allelopathic capabilities (Sing et al., 2016; Schat et al., 2011; Van Hezewijk et al., 2010). The improved fitness over native vegetation is evident by the extent to which *L. dalmatica* has reached in North America since its introduction (Figure 1). The waxy leaves and stems of *L. dalmatica* hinder conventional treatment methods, such as chemical and mechanical control, along with the ability to reestablish from severed roots as small as 1 cm. Biocontrol uses natural enemies from *L. dalmatica*'s native range in the Mediterranean to combat the spread. The natural enemy, *M. janthiniformis*, a stem-mining weevil, has adapted over time to be highly selective for *L. dalmatica*, with *M. janthiniformis* able to reduce populations of *L. dalmatica* throughout North America (Van Hezewijk et al., 2010; Smith et al., 2021; Weed et al., 2018). However, the degree to which *M. janthiniformis* successfully controls populations of *L. dalmatica* depends on the environmental conditions present at those locations (McClay & Hughes, 2007; Smith et al., 2021). This dependence on environmental conditions allows for the creation of habitat suitability models to predict species distribution. Careful deliberation of these conditions must occur when considering locations for biocontrol releases to ensure they are effective. Creating habitat suitability models can help reduce the number of releases that never establish and thus help conserve resources.

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