

# Predicting yellow toadflax infestations in the Flat Tops Wilderness of Colorado

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**Abstract** Understanding species–environment relationships is important to predict the spread of non-native species. Yellow toadflax (*Linaria vulgaris* Mill.) is an invasive perennial recently found in the Flat Tops Wilderness of the White River National Forest on the western slope of the Colorado Rocky Mountains. We hypothesized yellow toadflax occurrence could be predicted from easily measured site characteristics. We used logistic regression with stepwise selection to generate a model to predict yellow toadflax occurrence on a particular plot based on that site's physical characteristics. The experimental design was a paired-plot study in two locations using circular 1,018-m<sup>2</sup> plots. Sixty-eight plots that did not contain yellow toadflax and 65 plots that contained yellow toadflax were sampled at the Ripple Creek site in 1999. In 2000, 54 non-toadflax

plots and 55 toadflax-containing plots were sampled in the Marvine Creek site. Site characteristics sampled included: vegetation type; under-canopy light level; slope; aspect; soil properties; presence of disturbance, trails, and/or water; and total species richness. A model that correctly classified >90% of the 242 plots sampled included two vegetation type parameters, the presence of trails, and total species richness. Yellow toadflax is most often found in areas that were open-canopy sites, along trails, and with higher species diversity plots (>23 species). This approach can be used for other species in other areas to rapidly identify areas vulnerable to invasion.

**Keywords** Early detection · Habitat vulnerability · Invasive species · Predictive modeling · Rapid assessment

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## Introduction

Thousands of non-native plant species from other countries have spread across the United States, generally in a predictable broad-scale pattern. Counties high in native species richness (or density; number of species/km<sup>2</sup>) had higher significantly higher non-native species richness compared to species-poor counties (Stohlgren et al. 2003, 2006a). This general pattern of invasion has also been reported at plot scales (1–1,000 m<sup>2</sup>) for

many vegetation types in the United States (Stohlgren et al. 2006b). Still, little was known about the spread of individual species at local scales to corroborate these general patterns, particularly early in the invasion process.

Yellow toadflax (*Linaria vulgaris* Mill.) is an exotic perennial of the family Scrophulariaceae (Weber and Wittmann 2001) introduced to North America by European settlers as early as the late 1600s (Mitich 1993). Yellow toadflax quickly escaped cultivation and became established throughout the United States and Canada (Saner et al. 1995; USDA, NRCS 2002). Only recently has yellow toadflax become a concern to land managers in the northern Great Plains and high-elevation areas Intermountain West. Yellow toadflax readily establishes in a variety of habitats from dryland cropping systems in Saskatchewan (Saner et al. 1995) to alfalfa fields and sub-irrigated meadows in the Rocky Mountain region (J. R. Sutton, Colorado State University, personal observation). In Colorado, yellow toadflax is now spreading from 2,000 m to above timberline in the relatively un-invaded sub-alpine tundra at over 3,650 m (J. Connor, Rocky Mountain National Park, personal communication). On the Western Slope of the Colorado Rocky Mountains, yellow toadflax has begun to invade designated wilderness areas where minimal human impact has occurred. The invasion of yellow toadflax into wilderness areas is of great concern to those responsible for managing these areas (Thomas McClure and Harold Pearce, White River National Forest, Rio Blanco District, personal communication).

A more complete understanding of yellow toadflax distribution and spread is necessary to further develop effective management practices and control measures. In addition, identifying physical characteristics common to areas infested with yellow toadflax will allow land managers to direct monitoring and management resources to areas that are most likely to contain yellow toadflax, increasing the efficiency of these activities over large areas. Control programs for yellow toadflax are still being developed. Efficacy of chemical control is highly variable from site to site and even from patch to patch (Sebastian and Beck 1998a, b, 1999); and the large-scale effect of

biocontrol agents, despite established populations and documented impact (Saner et al. 1995), has not been demonstrated (LaJeunesse 1999). In any case, we need better information on the vulnerability of different sites to invasion to target populations while they are small and affordably treated (Rejmánek and Pitcairn 2002).

The use of site characteristics to identify areas likely to be infested with noxious weeds has proven useful for spotted knapweed (*Centaurea maculosa* Lam.) and Eurasian watermilfoil (*Myriophyllum spicatum* L.) (Chicoine et al. 1985; Buchan and Padilla 2000); but to our knowledge, no attempt has been made to identify areas most likely to contain yellow toadflax early in the invasion process.

We hypothesized that yellow toadflax occurrence could be predicted in the Flat Tops Wilderness in the White River National Forest on the western slope of the Colorado Rocky Mountains by easily measured site characteristics. To test our hypothesis, we recorded the characteristics of 120 plots containing yellow toadflax and 122 randomly chosen plots without yellow toadflax divided among two sites. A logistic regression model identified the most significant physical factors across both sites conducive to yellow toadflax occurrence, and predicted the probability of yellow toadflax occurrence with easily measured site characteristics.

## Materials and methods

### Sampling strategy

We conducted sampling at two sites within the Flat Tops Wilderness of the White River National Forest, located on the Western Slope of the Colorado Rocky Mountains during the summers of 1999 and 2000. These sites were selected to represent a continuum from recently invaded sites (since the 1980s) to adjacent un-invaded sites. This provided us the opportunity to evaluate species–environment relationships and invasion success early in the invasion process. At each site, characteristics of plots infested with yellow toadflax were compared to plots without yellow toadflax.

### *Ripple Creek site*

In 1999, we sampled the Ripple Creek site located 55 km east of Meeker, CO. The site was ~2,600 ha composed primarily of spruce (*Picea engelmannii* Parry ex Engelm.)/fir (*Abies lasiocarpa* (Hook.) Nutt.) forest intermixed with aspen (*Populus tremuloides* Michx.) stands and large meadows. Elevations of sampled plots ranged from 2,699 to 3,180 m. Yellow toadflax infestations were primarily small (generally <math>\leq 0.1</math> ha) isolated patches with distinct borders. Very few individuals were found outside of patch borders in surrounding vegetation. Sixty-eight non-infested plots were sampled between July 8 and July 24. A total of 65 yellow toadflax infestations were identified and sampled between July 28 and August 06, representing many of the obvious infestations at the site.

### *Marvine Creek site*

In 2000, we sampled the Marvine Creek site, located ~13.5 km southwest of the Ripple Creek site. The Marvine Creek site consists of a glacial valley ~7.5 km long and 1.5 km wide bisected by Main Marvine Creek. The valley walls predominantly consist of spruce/fir forest intermixed with aspen stands. The valley floor is relatively timber free to the north but narrows to the south and becomes intermittently closed by timber nearing Lower Marvine Lake. Elevations of sampled plots ranged from 2,519 to 2,877 m. Extensive yellow toadflax infestations (diffuse, >0.5 ha patches) at the Marvine Creek site drastically reduced the number of non-infested plots sampled, and made accurate size estimates of most yellow toadflax patches difficult to determine. Yellow toadflax in the Marvine Creek drainage has expanded from once discrete patches into a relatively diffuse infestation, often with obscure patch boundaries. Sampled toadflax patches were restricted to infestations with discrete borders that could be easily identified and sketch mapped. A total of 54 non-infested plots were sampled between July 16 and July 20. Fifty-five yellow toadflax patches were randomly selected from the total number of patches that were mapped and these were subsequently sampled. One infested plot was sampled

on July 16, due to location, and the remainder of the infested plots sampled from July 25 to July 28.

### Plot selection and design

We chose non-infested plots by randomly generating 100 points on a X, Y grid, overlaying the grid on a 1:24,000 scale United States Geological Survey topographical map of the site, and visiting all physically accessible points. Points not physically accessible were rejected. Points found to be infested with yellow toadflax were rejected as non-infested plots, and subsequently recorded as yellow toadflax infestations. To reduce variation in percent cover estimates over the sampling period, sampling was delayed until the majority of yellow toadflax had reached the bud growth stage.

### *Plot measurements*

Plots consisted of an 18-m radius circular plot totaling 1,018 m<sup>2</sup> with three transects radiating from the center. This slightly larger plot compared to many studies (e.g., Stohlgren et al. 2006b) was selected to better monitor spread in the future, but the general plot layout conforms to standard techniques (Barnett et al. 2006). Latitude, longitude, and elevation of each plot were recorded with a Trimble GeoExplorer II GPS when satellite reception allowed or estimated from topographical maps when satellite reception was not adequate. A 2.5-cm diameter × 30-cm long soil core was taken from along each of three randomly placed transects radiating from each plot center. The resulting cores were pooled for a composite soil sample of each plot. Degrees of slope was visually estimated to the nearest 5°, and later transformed with a sine function to take into account the greater effect of minor changes in slope at lesser slopes than greater slopes (P. Chapman, Department of Statistics, Colorado State University, personal communication). We recorded aspect to the nearest compass degree, converted to degrees from south and transformed with a cosine function to estimate total sunlight for a plot. The presence or absence of permanent or semi-permanent surface water, disturbance, and trails were recorded. Disturbance consisted primarily of, but not limited to, burrowing mammal activity. This was separated from the

presence or absence of trails, because trails are more likely an important vector for dispersal. No motorized or wheeled vehicles are allowed in the Wilderness Area, so all trails were of footpath, livestock, or wildlife origin. The vegetative composition of each plot was grouped into one of three categories: meadow, consisting mainly of grass and forb species with little or no trees present; timber, consisting of continuous aspen and/or spruce/fir stands; and margins, which contained boundary areas between meadows and timber. Statistical considerations (i.e., restrictions in the number of levels for each parameter) made it necessary to group aspen and spruce/fir stands into one level (timber). Although in sampling, yellow toadflax was found a total of four times in aspen stands and none in spruce/fir stands. Light intensity in the plot was visually estimated and placed into one of three qualitative categories: full, defined as no obstruction of direct sunlight; moderate, slight obstruction of direct sunlight as experienced along margins; and partial, moderate to high obstruction of direct sunlight as experienced in dense timber stands. The total number of plant species within the plot (plot species richness) was recorded. In previous studies, we found that total species richness (native and non-native species) served as a surrogate measure of habitat heterogeneity and resource availability, and as an indicator of invasibility (Kumar et al. 2006; Stohlgren et al. 2006b). We used the Rocky Mountain Herbarium's Colorado vascular plant checklist to determine a species' origin as native or exotic (Hartman and Nelson 2001). In plots containing yellow toadflax, the total area of each infestation, whether fully or partially contained in the plot, was estimated as well as percent cover of yellow toadflax within the whole plot.

### Soil analysis

Soil samples were oven-dried and pulverized to pass through a ten mesh sieve (<2.0 mm). Carbon : nitrogen and percent organic matter were determined by a LECO CHN 1000 Analyzer (LECO Corp., St. Joseph, MI, USA). Particle size analysis was conducted by hydrometer method (Gee and Bauder 1986). To negate the effect of high-organic matter percentage on particle size analysis by the hydrometer method, samples

containing greater than 5% organic matter were treated with 30% hydrogen peroxide and heated to 90°C to oxidize excess organic matter according to Gee and Bauder (1986).

### Model development and selection

Statistics were based on a case paired study in two locations comparing characteristics of plots with or without yellow toadflax at the Ripple Creek and Marvine Creek sites. Statistical analyses were conducted using the SAS statistical package Version 8e (SAS 1999–2001). We used logistic regression (PROC LOGISTIC), a procedure that simultaneously evaluates combinations of numeric and qualitative variables to estimate the probability of a particular event; in this case, predicting the presence of yellow toadflax in a particular plot, based on that plot's characteristics.

The general equation used for logistic regression is:

$$p_i = \frac{1}{1 + e^{\beta_0 + \beta_1 x_{i1} + \dots + \beta_n x_{in}}},$$

where the resulting dependent variable ( $p_i$ ) is a probability that yellow toadflax will appear in a site with a given set of characteristics:

$$0 \leq p_i \leq 1.$$

Site characteristic variables for inclusion in model selection were:

1. Plant species richness.
2. Vegetation type (timber, meadows, or margins).
3. Trails (presence, absence).
4. Water (presence, absence).
5. Light level in plot (full, moderate, partial).
6. Site (Ripple Creek, Marvine Creek).
7. Visual disturbance (presence, absence).
8. Slope (included after a sine transformation).
9. Aspect (included after a cosine transformation).
10. Soil sand percentage.
11. Soil clay percentage.
12. Soil organic matter percentage.
13. Soil C : N.

In addition to the individual site characteristic variables, several two-way interactions were investigated including: interactions between site and vegetation type, disturbance, number of plant species, and trails; interactions between organic matter percentage and C : N, sand percentage, and disturbance; disturbance interactions with trails and C : N; and slope interactions with light level and aspect. Thus, for model selection there were 24 possible variables.

Forward, backward, and stepwise selection procedures were used with significance levels of parameter inclusion and exclusion from the model each set at  $p \leq 0.05$ . The resulting models for each selection procedure were evaluated using multiple criteria including: the corrected Akaike Information Criteria (AIC) parameters (Akaike 1981), total number of model parameters, number of significant model parameters ( $\alpha = 0.05$ ), visual inspection of the model fit, number of included interactions, and percentage of plots for which toadflax classification was correctly predicted at a threshold of  $p_i = 0.5$ .

#### Model validation

We cross-validated independent models from the two study sites using the percentage of plots correctly classified as the measure of model accuracy. Summary statistics on individual variables indicated differences of individual factors between yellow toadflax and non-yellow toadflax plots, including differences between sites. Multiple comparison analysis with mean separation using the Tukey–Kramer method (Tukey 1953; Kramer 1956); (PROC GLM,  $\alpha \leq 0.05$ ) identified differences between continuous variables. Variables with qualitative data were analyzed using stratified contingency tables with Cochran–Mantel–Haenszel statistics (Cochran 1954; Mantel and Haenszel 1959) and Breslow–Day tests (Breslow and Day 1994) at a significance level of  $\alpha = 0.05$  indicating dependency of variables.

## Results

We first describe the model selection process, and then provide an individual variable analysis,

focusing on trails and species richness, to complement model selection.

#### Model selection

Site data were pooled and forward, backward, and stepwise selection procedures in logistic regression were used to develop a model to predict the presence of yellow toadflax in a particular plot. Initial models derived from the three selection procedures included a slope parameter that was significant in all models; however, means separation by the Tukey–Kramer method indicated that there was no difference in the slope means of yellow toadflax plots and non-yellow toadflax plots at either site. In addition, there was no difference among means between sites. The inclusion of the slope parameter lowered the AIC in all models from 113 to 111, indicating an increased fit, but slightly decreased the number of plots correctly classified at  $p_i = 0.5$ . Because of the qualitative nature of visually estimating slope, coupled with the need for transformation of slope data, and the lack of improved predicting power of models including the slope parameter, the slope variable was manually removed from the variables available for model selection, and new models were generated with forward, backward, and stepwise selection.

The resulting models by all selection procedures were identical. In the backward selection procedure, an algorithmic solution issue was mentioned by the statistical software, implying that the validity of the resulting model was to some degree questionable. In contrast, forward and stepwise selections satisfied convergence criteria set by SAS in the development of the model.

The resulting model had an AIC of 113 and contained four parameters, with three of the parameters showing significance at  $\alpha = 0.05$ . Since three categories existed for vegetation type, two parameters were required for its representation in the model, one of which,  $x_{i2}$  was significant ( $P < 0.001$ ), and the other  $x_{i1}$  was of undemonstrated significance ( $P = 0.588$ ). The parameter  $x_{i3}$  describing the presence of trails was significant ( $P = 0.045$ ) as was the parameter  $x_{i4}$  describing total species richness ( $P < 0.001$ ).



The equation describing the resulting model is of the form:

$$p_i = \frac{1}{1 + e^{(10.0091 + 0.2400x_{i1} - 2.6579x_{i2} - 0.5145x_{i3} - 0.3994x_{i4})}},$$

where:

$$x_{i1} \begin{cases} -1 \text{ timber} \\ 0 \text{ meadow,} \\ 1 \text{ margin} \end{cases}$$

$$x_{i2} \begin{cases} -1 \text{ timber} \\ 0 \text{ margin,} \\ 1 \text{ meadow} \end{cases}$$

$$x_{i3} \begin{cases} 1 \text{ trail present} \\ -1 \text{ trail not present} \end{cases}$$

$$x_{i4} \text{ \{number of species per plot.}$$

With a classification threshold set at  $p_i = 0.5$ , the model correctly classified >90% of the plots as containing or not containing yellow toadflax. The majority of the misclassifications at both sites were plots that had a probability of yellow toadflax in the  $0.25 \geq p_i \leq 0.75$  range with few misclassifications when  $p_i \leq 0.25$ , and  $\geq 0.75$ ; indicating the majority of plots with a high or low probability of yellow toadflax were correctly identified (Table 1).

According to the model, if a plot is located in a meadow, along a trail, and has a total of 15 species, there is >25% probability that yellow toadflax is present. The probability increases to >50% if there are 18 species present, and is >75% when 20 species are present. When the number of species per plot located in a meadow and along a trail is more than 23, there is greater than a 90%

probability of yellow toadflax presence in that particular plot.

### Individual variable analysis

#### Vegetation type

Cochran–Mantel–Haenszel tests showed a strong association between the presence of yellow toadflax and location in a meadow after adjusting for site ( $P \leq 0.001$ ). The percentage of plots in each vegetation type were tabled to better visualize the association between yellow toadflax occurrence and vegetation type (Table 2).

#### Trails

The trail variable was analyzed in SAS with a stratified contingency table using Cochran–Mantel–Haenszel statistics, a relative risk option, and the Breslow–Day test to indicate associations between trails and yellow toadflax presence adjusting for site, estimate an odds ratio for the presence of yellow toadflax, and determine if there is a significant site difference in the odds ratios, respectively. Cochran–Mantel–Haenszel tests showed a strong association between the presence of yellow toadflax and trails ( $P < 0.001$ ) after adjusting for site, with the probability of yellow toadflax in a plot along a trail just over two times the probability of yellow toadflax in a plot not along a trail. The Breslow–Day test indicate that there is no significant site difference in the odds ratios ( $P = 0.066$ ). However, yellow toadflax in the Ripple Creek site has a stronger association with trails than yellow toadflax in the Marvine Creek site (Table 3).

**Table 1** Percentage of plots correctly classified by the yellow toadflax model at differing probability levels in the two study areas

Probability of yellow toadflax	Ripple Creek		Marvine Creek		Total Plots	
	Non-toadflax (%)	Toadflax	Non-toadflax (%)	Toadflax	Non-toadflax (%)	Toadflax
$0 < p_i \leq 0.25$	85.3	1.5	75.9	3.6	81.1	2.5
$0.25 < p_i \leq 0.50$	5.9	3.1	9.3	3.6	7.4	0.8
$0.50 < p_i \leq 0.75$	7.4	16.9	9.3	9.1	8.2	6.7
$p_i > 0.75$	1.5	78.5	5.6	83.6	3.3	90.0

**Table 2** Percentage of non-toadflax and toadflax plots found in each vegetation type in the two study areas

Vegetation type	Ripple Creek		Marvine Creek		Total Plots	
	Non-toadflax (%)	Toadflax (%)	Non-toadflax (%)	Toadflax (%)	Non-toadflax (%)	Toadflax (%)
Meadow	19.1	72.3	9.3	65.5	14.8	69.2
Margin	17.6	23.1	25.9	32.7	21.3	27.5
Timber	63.2	4.6	64.8	1.8	63.9	3.3

**Table 3** Percentage of plots containing trails before and after removal of timber plots in the two study areas

Vegetation Type	Trail present within a plot			
	Ripple Creek		Marvine Creek	
	Non-toadflax (%)	Toadflax (%)	Non-toadflax (%)	Toadflax (%)
Meadow + margin + timber	19.1	70.8	16.7	40.0
Meadow + margin	24.0	69.4	21.1	40.7

*Species richness*

Differences in species richness per plot were determined with mean separation by the Tukey–Kramer method (Table 4). According to the all models developed, total species richness in a given plot is a strong predictor of yellow toadflax occurrence. Plots containing yellow toadflax have higher numbers of species than plots that did not contain yellow toadflax.

The Marvine Creek site overall was more species rich with a mean species richness of 25.7 (±0.70 SE) compared to 22.2 (±0.64) at Ripple Creek. Despite the differences between sites, the trend of yellow toadflax infested plots averaging ten more species per plot than non-toadflax plots

holds true across sites. The model does not distinguish between native and exotic species, only total richness; however, we felt it was important to distinguish between native and exotic species richness outside the model to identify species composition trends. Total species richness was broken down into native and additional exotic richness, or the number of exotic species per plot excluding yellow toadflax. The Marvine Creek site was higher in native and additional exotic species richness, 21.4 (±0.55 SE) and 1.2 (±0.12) species per plot, respectively, compared to 15.8 (±0.45) and 0.7 (±0.07) at the Ripple Creek site, with yellow toadflax plots at each site more species rich in both native and exotic species than non-toadflax plots (Table 4).

**Table 4** Mean species richness per plot by species origin by vegetation type in the two study areas

Vegetation type	Species origin	Mean species richness per plot			
		Ripple Creek		Marvine Creek	
		Non-toadflax	Toadflax	Non-toadflax	Toadflax
Meadow + margin + timber	Native	12.2c (0.40)	19.6b (0.50)	18.2b (0.62)	24.5a (0.69)
	Exotic	0.3c (0.06)	1.2b (0.09)	0.5c (0.11)	2.0a (0.16)
	All species	16.7d (0.51)	27.9b (0.68)	20.8c (0.69)	30.5a (0.80)
Meadow + Margin	Native	11.9c (0.65)	19.3b (0.50)	20.6b (1.07)	24.6a (0.70)
	Exotic	0.5c (0.10)	1.2b (0.09)	1.1bc (0.26)	1.9a (0.16)
	All species	17.7c (0.79)	27.4a (0.65)	23.8b (1.17)	30.6a (0.81)

Standard error in parentheses. Means with the same letter within a row are not significantly different Tukey–Kramer  $\alpha = 0.05$  (±1 SE)

This indicates areas high in native species richness are also most heavily invaded by yellow toadflax and other exotic species.

## Discussion

The results of the model fulfilled the primary objective of this study; to develop a model that successfully predicts yellow toadflax occurrence in the study areas. In addition to predicting the presence of yellow toadflax, the model development and validation procedures identified characteristics that appear to be important for the potential of yellow toadflax to occupy an area at one or both sites sampled. Analysis and discussion of these characteristics allows a better understanding of possible requirements and habitat preferences of yellow toadflax, increases the utility of the model from exclusively prediction, and facilitates a more complete understanding of yellow toadflax habitat preferences.

### Vegetation type

Yellow toadflax infestations were strongly associated with meadow habitats, significantly reducing the area needed to be monitored for yellow toadflax infestations. However, the specific conditions that encourage the association with meadows could not be specifically isolated. Brothers and Spingarn (1992) showed that forest fragments in old-growth forests of Central Indiana appeared to be resistant to invasion, and the frequency of exotics dropped sharply as one moved inward from forest edges. They hypothesized low-light availability was the main factor limiting invasion, but that limited propagule dispersal and low-disturbance levels may also contribute (Brothers and Spingarn 1992). The role of these and other differences affecting yellow toadflax invasion into timber have yet to be identified.

### Trails

Trails and roadsides are often cited as suitable habitat for a number of invasive species (e.g., Watson and Renney 1974; Saner et al. 1995;

Sheley et al. 1999), but only a few studies have quantitatively demonstrated exotic species spreading from trails or roads into relatively undisturbed habitats (e.g., Tyser and Worley 1992; Harrison et al. 2002). Yellow toadflax infestations within our study area were positively correlated with trails, and trail presence was included as a significant variable in the Ripple Creek and combined models. The role of trails in yellow toadflax dispersal within the Flat Tops area has not been determined. The seeds of yellow toadflax have been shown to be dispersed by wind, water, and ants (Ridley 1930; Lewis 1954; Zilke 1954; Häfliger and Brun-Hool 1976). Rodents have also been observed eating yellow toadflax seeds (Saner et al. 1995), and on more than one occasion we observed horses browsing yellow toadflax shoots and depositing un-eaten shoots further along the trail as they progress (J. R. Sutton, Colorado State University, personal observation). Dispersal would occur by this manner if shoots were browsed at a time that seeds were present on the un-eaten shoots. In addition to horse and wildlife movement and dispersals by mechanisms associated with those species, trails could aid seed dispersal by presenting a relatively compacted, obstruction free path for seeds to be blown along. Water runoff on trails could potentially carry seeds. Although there was no significant difference in the association of yellow toadflax and trails between the two sites, the Ripple Creek site had a higher percentage of toadflax plots located along a trail. One explanation for the differences among sites may be the amount of time since initial invasion at each site. The Marvine Creek site was most likely invaded by yellow toadflax sometime before the Ripple Creek site, which was probably invaded in the early 1980s (T. McClure and H. Pearce, White River National Forest, Rio Blanco district, personal communication). If trails are avenues of dispersal for yellow toadflax seeds by whatever mechanism, founding patches in the Marvine Creek site initially established along trails may have had enough time to move away from the trail into surrounding vegetation. The Ripple Creek site, being invaded sometime later, may still be in the initial invasion stages with infestations primarily established along the dispersal



corridor. Other factors important to invasion such as propagule pressure, soil disturbance by small mammals, and microsite variation were beyond the scope of this study.

### Species richness

There are several theories regarding the effect of species richness and the ability of an ecosystem to resist invasion. One paradigm is that habitats of low-plant diversity are more vulnerable to plant invasions than areas of high diversity (Elton 1958). This theory contends areas of high diversity are able to resist invasion by the process of competitive exclusion (Grime 1973), with native species capturing all available resources and preventing the establishment of additional species. This idea is generally supported by a number of small-scale highly manipulative studies (e.g., Tilman 1999; Naeem et al. 2000; Dukes 2002; Kennedy et al. 2002), and has been used in the development of successional weed management practices (Sheley et al. 1996). A number of other studies at multiple spatial scales indicate areas of higher diversity are more likely to be invaded by exotic species (e.g., Wiser et al. 1998; Smith and Knapp 1999; Stohlgren et al. 1999, 2003, 2006a, b; Levine 2000). These studies suggest that high-species richness does not ensure complete use of all the available resources, stability, or resistance to invasion (Stohlgren et al. 1999). Our study supports the latter hypothesis by illustrating native species rich areas in the study area are more likely to be invaded by yellow toadflax, as well as, other exotic species. In addition, the differences in species richness between yellow toadflax and non-toadflax plots are significant enough that species richness, along with location in meadows and the presence of trails, provided enough information to correctly identify the presence or absence of a single invasive exotic, yellow toadflax, in >90% of the plots sampled. While the exact mechanisms causing these patterns are poorly understood, species rich areas often have more higher habitat heterogeneity and available resources (e.g., light, water, warm temperatures, nutrients) than species-poor sites (Stohlgren et al. 2006a, b).

### Conclusions

Our model allows identification of particular locations vulnerable to invasion by yellow toadflax. This knowledge will aid early detection of incipient infestations and provide the opportunity to implement control measures when the probability of success is greatest. In addition, land managers will be able to estimate the percentage of land in a particular management unit that has the characteristics most often associated with yellow toadflax. This information could be important in assigning priority to yellow toadflax control in a particular area. If an area has few locations that have a high probability of yellow toadflax occurrence, management efforts may be focused on other species that have a greater impact in that particular area. If an area has a large percentage of locations where yellow toadflax occurrence is highly probable, management of yellow toadflax may be a top priority to prevent large-scale yellow toadflax infestations.

The strong positive association with yellow toadflax and trails suggest that new infestations in relatively un-invaded areas are most likely to occur along trails. Proper training of individuals, such as wilderness rangers and trail crews, in yellow toadflax identification could improve the efficiency of large scale monitoring efforts by utilizing individuals who are traveling the trails for other responsibilities. Our findings that yellow toadflax, as well as other exotic, are most likely to be found in areas of higher native species richness indicates yellow toadflax management practices must be considered in areas where native species diversity is a priority.

The broad ecological amplitude of yellow toadflax makes it unlikely that any model will accurately predict the occurrence of the species in all locations, but the model we developed may be used as a framework to determine important factors to predict the species in specific locations. As more information is collected in multiple locations and ecosystems, a better understanding of the most important environmental factors influencing yellow toadflax occurrence can be achieved.

## Summary

The results of this study identify physical site characteristics that appear important to yellow toadflax infestations in the study areas, and provide land managers a tool in the development of a more complete management strategy for yellow toadflax. Results showed that associations were not always consistent from site to site and further evaluation and validation of this model, by characterizing infestations not included in the model development at locations both within and outside of the Flat Tops Wilderness, is needed for a deeper knowledge of the site requirements of yellow toadflax. Our results may be used as a framework to determine the strength of the associations we identified in the study area with yellow toadflax infestations elsewhere; increasing our overall knowledge of yellow toadflax and the locations it is most likely to occur (i.e., in hot spots of plant diversity, along trails, and near current infestations). This information should help local weed managers in the early detection and rapid response of new infestations. This approach also could be applied to many other species and areas.

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