

THESIS

USING ECOLOGICAL NICHE MODELING TO IDENTIFY THE POTENTIAL RANGE OF
NOVEL INVASIVE TOADFLAX GENOTYPES IN THE U.S. NORTHERN ROCKIES

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2017

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ABSTRACT

USING ECOLOGICAL NICHE MODELING TO IDENTIFY THE POTENTIAL RANGE OF NOVEL INVASIVE TOADFLAX GENOTYPES IN THE U.S. NORTHERN ROCKIES

Dalmatian toadflax (*Linaria dalmatica* [L.] Mill.) and yellow toadflax (*Linaria vulgaris* Mill.) are vigorous invasive weeds posing significant management challenges. Predictions of suitable environments for these aggressive, emergent hybrid taxa are urgently required. Publishing predictive maps of the potential geographic distribution of toadflax will facilitate weed and land managers' efforts in maximizing limited resources for locating and controlling present and future populations of these invaders. The invaded ranges of Dalmatian and yellow toadflax span the Intermountain West, which encompasses the study area (i.e. Montana, Wyoming, and Colorado). These two species are listed as noxious weeds in all three states, with legal requirements for control in Wyoming and Colorado. Their hybrid progeny have even greater invasive potential; yet, relatively little is known about the current distribution of – and management approaches for – the hybrid. Ecological niche modeling with MaxEnt was performed for each taxon to identify favorable environmental characteristics and to predict fundamental niches in the study area. Areas at high risk of hybrid invasion were identified based on: a) known hybrid occurrence and associated environmental conditions; b) zones environmentally suitable for co-occurrence of the parental species; and c) areas common to both a) and b). Hybridization hot spots were predicted for western Montana; northwestern, northeastern, and southeastern Wyoming; and the Western Slope and Front Range of Colorado.

Model output also indicated that hybrid toadflax would have greater ecological amplitude than its progenitors, with potential hybrid invasion in much of north central Montana where the parental species have not been reported. These methods for predicting the distribution of an emerging hybrid taxon with little occurrence data can be applied to similar taxa. Managers working to control the spread of toadflax can use these results to prioritize areas of high invasion risk. To solicit feedback from those involved with managing toadflax, seven people were interviewed regarding their level of knowledge of hybrid toadflax and the usability of the maps. There was a lack of awareness among interviewees regarding the potential geographic spread of the hybrid, and there were six requests for localized hot spot maps. By generating predictive maps of hybrid toadflax distribution and reaching out to weed and land managers, awareness of this taxon will increase and managers will be attentive to ongoing biocontrol and herbicide research.

ACKNOWLEDGEMENTS

KM received Fellowship funding from the Colorado Mountain Club Foundation (<http://www.cmc.org/About/CMCFoundation.aspx>) and scholarship funding from GIS Colorado (<http://giscolorado.org/scholarships/>). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. I thank different organizations that requested individuals to share toadflax occurrence data with us, and the twenty contributors that did; these data certainly improved the quality of the models. I also thank Randall Boone for reviewing the map products and Jordan Lestina for contributing to the modeling.

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Chapter One: Introduction and Review of Literature

Introduction

Invasive species impact native species through competition and/or modification of habitat that renders it less suitable for the native (Wilcove et al. 1998; Hall and Ayres 2009). Invasive plants and animals cost the United States an estimated \$120 billion per year from environmental impacts and management efforts (Pimentel et al. 2005). A significant challenge in managing invasive plants is preventing their spread into new landscapes. To mitigate invasions, managers rely on early detection and rapid response (EDRR) programs, which involve eradicating new infestations prior to establishment. Early detection of infestations is more effective when informed by knowledge of conditions that promote species invasions (Bradley and Marvin 2011). Ecological niche models can generate predictions of suitable environmental conditions and geographic ranges such as for invasive plant species. Accordingly, these models can inform weed and land managers about the most suitable locations to employ EDRR programs. Maximum entropy (MaxEnt) is the modeling application used in this research. MaxEnt generates an environmental suitability map showing the likelihood of species occurrence across the study area (Phillips and Dudik 2008). Additionally, it works with occurrence-only data, as available for our selected taxa.

Our study system consists of three invasive plant taxa - Dalmatian toadflax (*Linaria dalmatica* [L.] Mill) (DT), yellow toadflax (*Linaria vulgaris* Mill.) (YT), and their hybrids (*L. dalmatica* x *L. vulgaris*) (HT). These toadflaxes are herbaceous creeping perennial forbs (Saner et al. 1995) for which hundreds of thousands of dollars are spent annually on attempts to control DT and YT on public lands in the western United States alone (Ward et al. 2009).

Our study area consisted of the states of Montana, Wyoming, and Colorado, selected to provide a sample of DT and YT occurrence data across a region of management interest. Geographic features of the study area include the western Continental Divide running down the spine of the Rocky Mountains. These mountains encompass significant elevation differences and geographic variation, causing considerable local climatic variation. East of the mountains are plains regions in all three states, characterized by lower elevations, higher year-round mean temperatures, and a longer growing season (WRCC 2016). Elevation in the study area ranges from 550 – 4400 m (1800 to 14433 ft.), contributing to a heterogeneous climate. Soils vary considerably across the study area, e.g., in clay content – approximately 5% in northwestern Montana up to nearly 60% east of the Rockies, also in Montana (soilgrids.org 2017). Clay content is lower in the mountains and higher in lower elevations across the study area. Total annual precipitation in the form of rain and snow is heterogeneous throughout the three-state area as well, ranging from highs of approximately 290 cm in the mountains to lows of less than 14 cm in southwestern Wyoming and southcentral Colorado (ClimateWNA 2017). The most prevalent land uses and land cover in the study area are coniferous forest, grazed rangelands, farming, and developed urban locations, representing a spectrum of ecosystems and therefore plant communities (USDA 2012).

Dalmatian toadflax history and biology

Originally from the dry climate of the Mediterranean region, DT was introduced to North America by the late 1800s as an ornamental plant (Vujnovic and Wein 1997). DT can tolerate a wide range of environmental conditions, contributing to its invasive success. In North America, it occurs at latitudes between 33° to 55° N (Vujnovic and Wein 1997). DT is usually found in

areas with dry summers and well-drained soils (De Clerck-Floate and Richards 1997; Lajeunesse 1999). Soils invaded by DT range from sandy loam to coarse gravel (Alex 1962).

DT flowering typically occurs from May through early August (Saner et al. 1995) and a mature plant can produce up to 500,000 seeds annually (Robocker 1974). This copious seed production makes DT highly competitive and able to invade cropland and un-grazed vegetation (Vujnovic and Wein 1997). DT seed has a lower proportion of dormancy and higher germination rates than YT seed (Morishita 1991), although dormant seed can persist for up to a decade, creating lasting management issues (Turner 2012). DT has an extensive root system – growing up to 1.8m deep and spreading to 3.6m horizontally, with semi-woody roots that produce adventitious buds (De Clerck-Floate and Harris 2002). Adventitious buds arise on rhizomes as soon as 9 weeks after germination; these buds generate independent daughter shoots in autumn that number up to 40 (Alex 1962). During the winter, DT persists as a rosette above ground from which stems regrow in the spring (Sing et al. 2016). DT may be especially competitive with winter annuals and shallow-rooted perennials (Sing and Peterson 2011) because the roots of mature plants are able to capture limited soil water (Coupland et al. 1963).

Yellow toadflax history and biology

YT is native to northern/temperate Eurasia (Chater et al. 1972) – a wetter climate than where DT originates. Introduction of YT to the United States occurred as early as the late 1600s, also as an ornamental plant, as well as a fabric dye and for medicinal purposes (Arnold 1982). It is prescribed today for jaundice, liver troubles, and various skin conditions (LeStrange 1977). Locations commonly invaded by YT include roadsides, railroads, abandoned areas, dry fields, grain fields, gardens, pastures, and other cultivated fields (Reed and Hughes 1970). YT prefers moderately humid sandy loam soils that are moderate to rich in nutrients and minerals (Hartl

1974), occurring in moist soils such as those associated with riparian areas (De Clerck-Floate and Richards 1997).

YT flowers from July through September (Saner et al. 1995). Reproduction in YT occurs both sexually by seed and asexually by adventitious root buds from the lateral and tap roots (Salisbury 1942; Bakshi and Coupland 1960). YT, as well as DT, are obligate outcrossing species (i.e., they introduce unrelated genetic material into a breeding line) fertilized by insects (Bruun 1937; Arnold 1982; Docherty 1982). YT is a difficult invasive plant to manage because of its morphological plasticity, perennial habit, and high degree of genetic variation (Zilke 1954; Saner et al. 1995; Lajeunesse 1999). Nadeau et al. (1991) performed a study showing that a YT plant with 10 cm roots and 10 cm shoots grew to a patch 2 m in diameter in one growing season. Once established, YT colonies persist mostly via seed production (Lehnhoff et al. 2008). Individual seed capsules contain 10 to 110 seeds, with 1,500 to 20,000 - 30,000 seeds produced annually per mature plant (Saner et al. 1995; Wilson et al. 2005). Asexual reproduction may start as soon as 2-3 weeks after germination (Zilke 1954). In their first year, plants can produce 90 to 100 secondary shoots from roots and in their second year, 200 to 250 shoots (Salisbury 1942; Zilke 1954). YT stems completely die back in winter; spring regrowth occurs only from sub-soil root buds (Sing et al. 2016). These characteristics of more rapid growth plus higher numbers of shoots produced result in YT being a more formidable invader than DT.

YT has a strong competitive ability and can rapidly expand, enabling it to markedly affect ecosystems. Once established, YT expands the quantity and density of patches and increases its ramet density within patches, affecting native plant communities (Pauchard et al. 2003) and potentially creating a monoculture (Lajeunesse 1999). YT also invades diverse ecosystems with high species richness (Sutton et al. 2007) and displaces desirable vegetation,

plus it decreases the carrying capacity and the appraised value of infested ranch land (Lacey and Olsen 1991). Lehnhoff et al. (2008) studied YT in a U.S. wildland setting and observed its ability to colonize and displace native vegetation in intact habitat. An invasion of YT in West Yellowstone National Park shows that it is a threat to both low-elevation disturbed lands and remote, high-elevation protected areas (Pauchard et al. 2003).

Noxious classification of toadflax

Toadflax are considered noxious because they are long-lived perennials that are difficult to eliminate once established. DT and YT are designated category 1 noxious weeds in Montana; reducing infestation and spread is acknowledged to minimize economic and environmental impacts (WMTF 2008). In Wyoming, both taxa are listed as noxious weeds, requiring a program for their control (WWPC 2016). In Colorado, both taxa – as well as the hybrid taxon – are on the noxious weed list B, mandating their spread be stopped (CWMAa, CWMAb 2016). DT and YT are also listed as noxious in Idaho, Nevada, New Mexico, Oregon, South Dakota, and Washington; DT alone is listed in Arizona, California, and North Dakota (USDA PLANTS Database 2017). The range of YT has been expanding in the Intermountain West, particularly Colorado, Idaho, Montana, and Wyoming (Markin 2002; Beck 2010).

Hybrid toadflax

Species hybridization has been suggested to increase invasive adaptations that are recognized as a mechanism of initiating and expanding invasions (Schierenbeck and Ellstrand 2009). Observed outcomes of plant hybridization also include the formation of a stable hybrid zone (Ferdy and Austerlitz 2002). The hybridization zone is of concern because it is an area in which the hybrid and both parental species coexist and greater numbers of hybrids may result. Hu (2005) proposed two different mechanisms for the maintenance of a hybrid zone: (1) an area

where hybrids are maintained by ongoing immigration of the parental gametes and (2) a superiority zone where hybrids are better adapted than either parental species.

Research has confirmed that hybridization is occurring between highly invasive populations of DT and YT, and that the hybrid progeny are viable and fertile. Yet the first records of hybrid toadflax in North America were not made until 2009 (Sing et al. 2016). The native ranges of these toadflax species do not overlap (Ward et al. 2009), which precludes hybridization in these environments. HT has been found in disturbed sites suitable for either parental species, including pastures, and rangeland in a variety of soils and climatic conditions (Sing et al. 2016).

The timing of both flowering and seed reproduction of DT and YT vary within the study area; however, due to the long duration of bloom cycles the likelihood of flowering overlap is high (Turner 2012) and the window for hybrid pollination is approximately 1.5 months. Pollinators may source pollen from DT or YT and then travel to a colony of the other taxon. Common strong-flying insect pollinators of toadflax such as bumble bees (De Clerck-Floate and Richards 1997) can travel over 1.5 km between pollen sources (Osborne et al. 2008). Accordingly, the hybrid could establish via bee pollination within a parent colony at sites suitable to both DT and YT (Ward et al. 2009).

Greenhouse-based experiments at Colorado State University and long-term field monitoring of toadflax invasion in the Helena and Beaverhead-Deerlodge National Forests in Montana show that hybrid toadflax can outcompete and replace DT and YT (Brenner and Ward, unpublished data; Sing, unpublished data). Toadflax hybridization is of notable concern because of the occurrence of heterosis (“hybrid vigor”) whereby the hybrid taxon is a more robust and aggressive invader than either of its parental species (Turner 2012). One common garden study

yielded preliminary results indicating that HT demonstrates greater growth and reproductive potential compared to either of the parental species (Turner 2012). Examples of heterosis in weedy species have also been reported in *Tamarix* in North America (Gaskin and Schaal 2002) and *Fallopia* in Europe (Tiebre et al. 2007).

Management challenges from hybridization in invasive plants

Invasive plant hybrids threaten native communities and are difficult to control for land managers (Vilà et al. 2000). The difficulties arise from diverse aspects of management: identification, novel genetics, efficacy of biocontrols and herbicides, and altered phenology in hybrids.

Cryptic hybridization makes identifying hybrids difficult as most closely resemble one of the parental taxa despite genetic variation, and hybrids may exhibit a sparse geographic distribution while emerging as a novel population. Boswell et al. (2016) found that introgression of YT genes into DT populations (i.e. cryptic hybridization in DT) may be more widespread than previously realized, complicating the identification, and therefore taxonomy, of invasive DT in North America. Their research showed that some populations presumed to be DT may be backcrossed hybrids that have regained many morphological and ecophysiological traits of DT while possessing introgressed YT genes. A previous study by Ward et al. (2009) also reported difficulties distinguishing DT from HT. Plants resembling DT – except with narrow leaves – have been confirmed as HT (Ward et al. 2009) or as drought-stressed DT (S Ward and S Sing, personal observation). Recurrent backcrossing between HT and the parental species results in a spectrum of genetic makeup and therefore morphological characteristics of HT ranging from DT-like to YT-like. This spectrum underpins the difficulty of identifying HT in the field. Public lands in the United States such as wilderness areas and national parks commonly do not have the

resources for field crews to search extensively for species of concern. Thus, many weed populations remain undetected until invasions become much more widespread (Mack et al. 2000).

Williams et al. (2013) found that genetic differentiation in *Tamarix* species (*T. ramosissima* x *T. chinensis*) emphasizes the impact of plant hybridization and may explain the different degrees of success of biocontrol agents. Depending on location in the western United States, genetic variation due to hybridization resulted in variable susceptibility to biological control. Increased levels of *T. ramosissima* introgression was found to be highly correlated with greater vulnerability to insect attack (Williams et al. 2013). Applying knowledge of factors influencing biocontrol susceptibility, e.g., variability in location and hybridization with *Tamarix*, demonstrably improved the efficiency of management tactics. Parepa et al. (2013) found that invasive knotweed hybrids (*Fallopia japonica* crossed with *F. sachalinensis* yielding their hybrid *F. bohemica*) are more competitive than their parental species, and hybridization significantly increased their invasiveness. The authors concluded management efforts of knotweed hybrids should be prioritized over the parental taxa because the hybrids are inherently the most vigorous of the invasive knotweeds. Hybrid knotweed is another taxon exemplifying the relationship between genetic novelty in weeds and increased management challenges.

DT and YT are obligate outcrossers which maintain high genetic diversity (Mitich 1993). Gene flow between DT and YT could result in multiple outcomes: novel genetic combinations may enable hybrid taxa to outcompete and even displace their progenitors (Buerkle et al. 2000) or they may evolve an ecological amplitude beyond the limits of their parental species (Barton 2001). The deep and extensive root systems of DT and YT allow them to withstand many different control methods (Saner et al. 1995) and the efficacy of biocontrols on HT is not yet

known. Hybridization in plants can also cause a change in phytochemical compounds (Cheng et al. 2011), which may make them unrecognizable or unpalatable to specialized herbivores that use plant chemistry to recognize suitable host species (Schoonhoven et al. 2005). The stem-boring weevils *Mecinus janthiniformis* and *Mecinus janthinus* are effective biocontrols on DT and YT, respectively. Unfortunately, each of these weevil species has a strong preference for its natural host toadflax. It is currently unknown if the weevils will establish on and control HT populations (Boswell et al. 2016; S Sing 2017, personal communication).

In addition to challenges presented by biocontrol, herbicide application to treat toadflax in the study area is rife with difficulty. Spraying herbicide, unless timed perfectly, has limited impact on both DT and YT (S Sing 2017, personal communication). When considering the various land cover types inhabited by toadflax, especially in the backcountry, applying herbicides can be impractical and uneconomical against very large infestations. Off-target damage from herbicide application may also negatively affect native plant communities in the long term (Sing et al. 2016). YT is more difficult to treat with chemical controls than DT as YT shows limited and variable response to herbicides (Sebastian and Beck 1998, 1999). The first known garden study of herbicides on HT began in September 2016 in Montana. Results showed a comparatively high survival rate of HT at both the full and half rate picloram treatments, likely conferred by the genetic contribution of YT rather than DT (S Ward and S Sing 2017, personal communication). Achieving less than 100% eradication of any of these toadflax taxa may result in selection of individuals with a degree of resistance to the herbicides.

Weber and D'Antonio (1999) compared the invasiveness of hybrids to their parental species and found hybrids can be more plastic and more tolerant of environmental variation. Turner (2012) describes the benefits of early emergence of plants in the spring: competitive

advantages such as having earlier access to resources, e.g. space and light, earlier flowering times that may alter the plant-pollinator interactions or other mutualisms, and avoiding late-season drought or frost. Lastly, earlier maturation of seeds resulting from completing the reproductive cycle more quickly could increase ecological amplitude in regions with shorter growing seasons. Turner (2012) performed a common garden experiment with replicated sites in Fort Collins, CO and Bozeman, MT including testing the emergence times of DT, YT, and HT. Hybrids generally emerged from winter dormancy earlier than either of the parental species. Although emergence time varied between sites and did not directly result in earlier flowering or seed set, HT emerging earlier may increase patch expansion by capitalizing on resources before DT and YT have an opportunity to make use of them.

Challenges presented by correct identification, novel adaptive genotypes, variable response to control methods, and altered phenology in toadflax hybrids support the predictive modeling of the invasive range of HT as it has the potential to be the most formidable toadflax taxon in the study region. These predictions will be communicated to weed and land managers, particularly in high-risk areas, to increase awareness of the potential for HT invasion and thereby improve the effectiveness of management.

Ecological niche modeling with MaxEnt

Ecological niche models (ENMs) – also known as species distribution models, bioclimatic envelopes, or correlative niche models – predict suitable range for a species based on correlated environmental variables at specified species occurrence locations. Ongoing advancements in geographic information systems (GIS) and greater availability of detailed geospatial environmental data, including remote sensing data, have led to the use of ecological niche modeling for numerous applications in ecological research (Guisan and Zimmermann 2000). The

ecological niche modeling process enables questions to be addressed about which environmental variables (e.g., temperature, precipitation, primary productivity, etc.) provide better explanations of observed species distributions (Hawkins et al. 2003) and can be used to contrast species' niches (Kremen et al. 2008). Quantitative modeling approaches are based on ecological niche theory and are applied to understand species-environment relationships (Lestina et al. 2016). An ENM incorporates species occurrence data with selected environmental variables to model a species' niche in environmental space, which is then projected into geographical space to predict the species' distribution (Elith et al. 2013).

MaxEnt is software that uses a machine-learning method to estimate the probability of a species presence across a given study area (Phillips et al. 2006). Species occurrence point locations and environmental GIS layers are input into MaxEnt; species absence data is not required. MaxEnt calculates the distribution of maximum entropy (i.e., that is most spread out, or closest to uniform) and produces an environmental suitability map that shows the probability of species occurrence throughout the study extent (Phillips and Dudik 2008). Thus, the final map shows a gradient between least-likely to most-likely locations of species presence. MaxEnt is increasingly used in a variety of applications, including risk of invasive species and pest establishment (Kumar et al. 2014), determining suitable habitat for threatened and endangered species (Kumar and Stohlgren 2009), and managing insect vectors of diseases (Larson et al. 2010). Elith et al. (2006) compared the performance of various ENM algorithms to produce guidelines for users as to which methods may perform better for their species-environment scenarios, and found that MaxEnt outperformed other evaluated modeling applications (Elith et al. 2006). MaxEnt is notably well suited for species with a small number of occurrence records, such as HT in this study (Benito et al. 2009). MaxEnt is the most commonly used ecological

niche modeling application for inferring species distributions, niches, and environmental tolerances (Warren and Seifert 2011).

There are some limitations with the MaxEnt ENMs in this study. Specifically, the model outputs do not consider (a) interspecific competition (b) presence/absence of biocontrol species (c) dispersal mechanisms carrying the hybrid beyond the occupied niches of the parental species (it is possible that HT may occur in niches where its parental taxa are not found based on propagule movement) (d) source-sink and metapopulation dynamics (Hanski 1999) and (e) environmental stochasticity. Lastly, predictions are based on presence data and environmental variables available from an historical window of time (1990 – 2016, and as old as 1991 and as new as 2015, respectively); therefore, predictions are most accurate for the present and not the future. Nevertheless, environmental suitability maps produced by MaxEnt showing invasive species' predicted distributions are valuable tools for resource managers to prevent the species from spreading and for designing effective EDRR systems (Peterson 2003).

MaxEnt modeling of invasive plants

Padalia et al. (2014) modeled bushmint, *Hyptis suaveolens* (L.) Poit., throughout India using MaxEnt and GARP (Genetic Algorithm for Rule-Set Production) with one objective being comparing the two modeling algorithms. MaxEnt and GARP were chosen because they have shown accurate prediction capabilities with occurrence-only data (i.e. no absence data) (Hijmans and Graham 2006; Phillips and Dudik 2008). The authors used 530 locations randomly collected with uniform sampling intensity, and with environmental variable selection – 14 predictors after reducing correlations. To run the models in a similar way, k-fold cross validation was used in MaxEnt and the best subset selection procedure was used in GARP (per Stockwell and Peters 1999; Anderson et al. 2003; Phillips et al. 2006). GARP results predict presence or absence in a

binary fashion; accordingly, a threshold procedure was applied to the MaxEnt outputs to convert them from continuous to binary. The area under the receiver operating characteristic curve (AUC) was used to evaluate model performance and robustness, as AUC is a widely used procedure for such comparisons (Phillips et al. 2006). The MaxEnt model produced a higher AUC – 0.86 – compared to that of GARP – 0.75. This demonstrates a stronger prediction capability of MaxEnt and suggests GARP did worse in discriminating suitable/unsuitable sites (Padalia et al. 2014). Additional studies similarly reported MaxEnt’s higher performance than other modeling applications (see Stockwell and Peterson 2002; Phillips et al. 2006; Babar et al. 2012).

O’Donnell et al. (2012) investigated potential hot spots of invasive plants in Australia using MaxEnt models. The authors selected 72 Weeds of National Significance to model; species occurrence data were sourced from an Australian herbarium and the Global Biodiversity Information Facility (GBIF). Given the creation of 72 models, environmental variables were held constant at seven total temperature and precipitation layers, which were downloaded from WorldClim.(O’Donnell et al. 2012). Variables were selected in advance that are important factors influencing the physiology and distribution of many plant species (Woodward 1987). Models were fit using occurrence data and environmental variable layers – both at the global scale, ensuring the broadest range of data was used (Broennimann and Guisan 2008; Beaumont et al. 2009) and subsequent analysis was performed by clipping Australia out of the global environmental suitability maps. This approach may result in less reliable and accurate maps at the scale of Australia (S Kumar, personal communication 2017). The authors applied a threshold to the suitability maps to create binary maps that estimate the boundaries of a species’ bioclimatic range; these suitability rasters were summed to produce an invasion hot spots map.

O'Donnell et al. (2012) predicted the southwest corner and southeastern Australia as hot spots for invasive plants.

MaxEnt modeling of hybrid invasive species

Although MaxEnt has been widely used for modeling invasive species occurrence, very few published studies have focused on using MaxEnt to predict hybridization and potential hybrid expansion in non-native invasives. Sánchez-Guillén et al. (2013) performed a MaxEnt modeling study on potential hybridization among *Ischnurid* damselfly species in the Mediterranean region. The authors used predicted environmental layers from three future climate scenarios in addition to the current climate layers to model predictions of niche shift under these scenarios. Reproductive isolation factors were also considered when the risk of hybridization was determined. Occurrence data from seven species of damselfly were used in the MaxEnt models, and a suitable/unsuitable threshold was applied to generate environmental suitability maps. Sánchez-Guillén et al. (2013) found that in the 2020 scenario, 10 pairs of *Ischnurid* damselfly species were predicted to increase their overlapping ranges, and five of those pairs were also predicted to hybridize. Given that this was a multi-species investigation considering different climate scenarios, hybridization hot spots were not mapped, likely because this would add complexity to the research.

Vardien et al. (2011) used MaxEnt to model distribution of *Lantana camara*, a shrub-like species that is a notorious global invader and is listed among the world's one hundred worst invasive species (Lowe et al. 2000). Invasive *L. camara* populations represent a complex of numerous horticultural hybrids and a small number of wild *Lantana* species (Sanders 1987, 2006) that display high morphological variation resulting from breeding and intra- and inter-specific hybridization (Spies 1984; Binggeli 2003). Vardien et al. (2011) used MaxEnt to

determine whether the current distribution of *L. camara* in South Africa constitutes a smaller realized climatic niche or the fundamental climatic niche. Their results identified suitable areas for expansion in the KwaZulu-Natal province midlands. Biocontrol of *L. camara* has been confounded by the diversity of *Lantana* hybrids. A biocontrol agent's preference for a specific *Lantana* host or hosts appears to limit its success (Zalucki et al. 2007), and Vardien et al. (2011) concluded that using spatial data to model invasion and determine the potential geographical ranges of *L. camara* is important to the management of the species.

Mukherjee et al. (2011) investigated whether hybridization was a driver behind niche shift in Brazilian peppertree (*Schinus terebinthifolius*) in the invaded range in Florida. The Brazilian peppertree is regarded as one of Florida's most widespread and damaging invasive plants, and extensive intraspecific hybridization between native range geographically and genetically differentiated biotypes has taken place there (Mukherjee et al. 2011). A common garden experiment showed that Brazilian peppertree hybrids have higher survival rates, growth rates, and biomass in Florida than parental biotypes (Geiger et al. 2011). Genetic divergence, which may occur during hybridization in an invasive species due to rapid evolution after introduction (Prentis et al. 2008), can cause a shift in the species' fundamental niche. To test for niche shift, the authors used MaxEnt to model reciprocal predictions of the distribution of Brazilian peppertree between native and invasive habitats: a model was created for South America and the suitable environment was projected onto Florida, and vice versa. This is done to evaluate the accuracy of transferring a model from one location to another, while keeping the species occurrence data constant. Mukherjee et al. (2011) used default MaxEnt settings, e.g., for features and regularization multiplier (but not for training-testing data split, replicate runs, random seeded subsample, and average of replicated predictions). Default settings in MaxEnt do

not always produce the best predictions (Merow et al. 2013; Kumar et al. 2014). Their results showed the reciprocal predictions of the current realized niche of the Brazilian peppertree haplotypes were inaccurate in either Florida or Brazil (Mukherjee et al. 2011). In conclusion, the small number of published studies to date indicate that predicting hybridization and potential hybrid expansion in non-native invasives is a relatively novel and unexplored use of MaxEnt.

Other toadflax modeling studies

Other authors have researched the potential range of DT or YT, and the environmental factors contributing to these distributions, using various modeling methods. However, no published research was found that modeled the geographic range of HT. The theme of predicting distributions is seen throughout, though at differing spatial scales and points in time and only with one toadflax species. Blumenthal et al. (2012) concluded that DT occurrence may be more common on steep slopes – especially south-facing – and that grazing may inhibit DT invasion. Multiple statistical models were employed to make these predictions; supporting data were from the High Plains Grassland Research Station in Wyoming. Pollnac et al. (2014) predicted DT population growth rate would not decrease with increased elevation based on population dynamics models and data from the Greater Yellowstone Ecosystem (northwestern Wyoming, southwestern Montana, and eastern Idaho). This suggests that DT could be occupying a realized niche below its upper elevation bound (Gaston 2003). However, the authors observed that DT germination rates decrease at the highest elevations studied, potentially due to a climatic limit (F. Pollnac and L. Rew, unpublished data). Sutton et al. (2007) predicted that YT is most often found in areas that were open-canopy sites, along trails, and with higher species diversity based on logistic regression models on data from plots at two sites in the Flat Tops Wilderness, Colorado. Xu (2015) used MaxEnt modeling to estimate the distribution of YT and 27 other

invasive alien species for both current and future bioclimatic conditions in the Chinese Upper Ili River Basin. The author's key findings were identifying the most important bioclimatic variables predicting species distributions – for YT, precipitation of the driest month, mean temperature of the coldest quarter, and mean annual temperature. The importance of understanding the potential distribution of DT and YT is demonstrated by these studies and, given the risk of HT being a greater invasive threat, considering the range of all three taxa is more exigent. From the preceding examples, clearly different modeling approaches are used to fit different needs, e.g., spatial and temporal scales, population biology characteristics, etc. We used MaxEnt to address different questions: What is the predicted distribution of HT based on either co-existence of DT and YT or from an HT-only MaxEnt model?

Research objectives

Our research objectives were to model predictive spatial distributions for DT, YT, and HT in Montana, Wyoming, and Colorado, and to solicit feedback from weed and land managers on the utility of these predictions.

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Chapter Two: Using Ecological Niche Modeling to Identify the Potential Range of Novel Invasive Toadflax Genotypes in the U.S. Northern Rockies¹

Overview

Dalmatian and yellow toadflax are both aggressively invasive weeds throughout the Intermountain West. The timely development of methods that accurately predict and efficiently detect the occurrence of their vigorous and fertile hybrid progeny is therefore critical. Generating model-based maps of potential toadflax genotype distributions will allow weed and land managers to maximize limited resources for locating and controlling these invaders. We used ecological niche modeling to identify environmentally suitable areas for these toadflax taxa in Montana, Wyoming, and Colorado. Areas at high risk of hybrid invasion were identified based on: a) known hybrid occurrence and associated environmental conditions; b) zones environmentally suitable for co-occurrence of the parental species; and c) areas common to both a) and b). These techniques allow comparison of different model outputs, especially relevant to modeling emerging invasives, such as novel hybrids, with minimal occurrence data. Areas identified through modeling approaches indicate where the risk of hybrid toadflax invasion is greatest, including parts of north central Montana where model output predicted the hybrid may spread without prior confirmed co-invasion of the parental taxa. Hybridization hot spots were predicted for western Montana; northwestern, northeastern, and southeastern Wyoming; and the Western Slope and Front Range of Colorado. Despite relatively few confirmed occurrences of hybrid toadflax to date, our model outputs indicate that hybridization is likely to be widespread

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in the studied area. Identifying areas of probable toadflax occurrence, especially areas at risk of hybrid invasion, will raise awareness of hybrid toadflax among land and weed managers, and enable them to more efficiently direct resources to scouting and appropriate control.

Management Implications

Dalmatian and yellow toadflax are long-lived and difficult to control non-native perennials found throughout much of North America. Both toadflaxes are aggressive invaders in western states, forming persistent colonies through creeping root spread and seed production. Hybrids of Dalmatian and yellow toadflax have greater growth and reproductive potential than either of the parental species, making them potentially more successful invaders. In this study, we modeled environmental suitability for all three toadflax taxa and mapped areas at risk of hybrid toadflax invasion in Montana, Wyoming, and Colorado. The locations of few hybrid toadflax populations have been confirmed to date; however, our model output shows the potential for widespread hybrid invasion. This modeling study will help managers identify areas where hybrid toadflax is most likely to occur and will allow them to direct limited resources more effectively to scouting for and controlling it. Raising awareness of hybrid toadflax and its potential geographic distribution is the fundamental initial step to improved management of this invasive threat.

Introduction

Invasive plants disrupt native plant communities primarily via resource competition, and potentially through habitat modification that renders it less suitable for native and other desirable species (D'Antonio et al. 2004; Wilcove et al. 1998; Hall and Ayres 2009). Invasive plants and animals cost the United States (U.S.) an estimated \$120 billion per year from environmental impacts and management efforts (Pimentel et al. 2005). Hybridization may increase the threat of

invasion by evolving fitter genotypes that can outcompete and displace the parental species in the invaded habitat: reported examples include *Spartina* (Ort and Thornton 2016), *Fallopia* (Parepa et al. 2014), and *Typha* (Zapfe and Freeland 2015). Additionally, hybrids may present the management challenge of correct target identification due to minimal morphological differences between hybrids and their parental taxa (Boswell et al. 2016; Olson et al. 2009) and a sparse distribution of emerging hybrid populations. Public managed lands in the United States such as national parks and national forests commonly lack staffing and funding resources to adequately search for species of concern. Thus, incipient populations often remain undetected until invasions become widespread and dominant (Mack et al. 2000; Maxwell et al. 2012; Rauber et al. 2016). Accurate spatial predictions of invasion, such as those generated by computer modeling, can provide a valuable management tool to reduce invader impacts before eradication of the species becomes unfeasible or prohibitively expensive (Koncki and Aronson 2015).

Dalmatian toadflax (*Linaria dalmatica* (L.) Mill.), yellow toadflax (*Linaria vulgaris* Mill.) and their hybrids (HT) are invasive plants in the U.S. Intermountain West and other regions of North America. Dalmatian toadflax (DT) is native to the Mediterranean (Alex 1962) and was introduced to the U.S. in the late 1800s (Vujnovic and Wein 1997). DT is classified as a noxious weed in seven states (USDA NRCS 2017). The native range of yellow toadflax (YT) is temperate Eurasia and it was brought to the eastern U.S. in the late 1600s (Mack 2003; Boswell et al. 2016). YT has invaded the lower 48 states, Alaska, and nine Canadian provinces and is listed as a noxious weed in eight states (USDA NRCS 2017). The native ranges of DT and YT do not overlap and hybridization between these congeners has not been reported in Eurasia (Sutton 1988). DT and YT are perennial forbs that usually colonize disturbed areas (Arnold 1982; Vujnovic and Wein 1997) though YT has also invaded intact native plant communities in

high-elevation wilderness areas (Sutton et al. 2007). These toadflax species are obligate out-crossers that can spread via roots and rhizomes (Saner et al. 1995; Vujnovic and Wein 1997), and both have high levels of intraspecific genetic diversity (Brown 2008; Ward et al. 2008; Boswell et al. 2016).

Hybridization is now recognized as a significant facilitator of plant invasion (Schierenbeck and Ellstrand 2009) and as a threat to native genotypes (Rhymer and Simberloff 1996). It is unknown when gene flow between DT and YT first occurred in our study area of Montana, Wyoming, and Colorado; these toadflax hybrids were confirmed relatively recently (Ward et al. 2009) and may be more widespread in plant communities, possibly for longer than previously realized (Boswell et al. 2016). Early generation hybrids between DT and YT produce vigorous and fertile progeny that are often morphologically distinct from either parental taxon. Hybridization of these parental species is of concern because both DT and YT are individually highly invasive, and their heterotic progeny are likely to be even more aggressively invasive. In a series of common garden experiments, hybrid toadflax genotypes outperformed the parental taxa across multiple vegetative and reproductive traits (Turner 2012). Additional consequences of toadflax hybridization include biological and ecological changes, as well as management challenges. Hybridization between DT and YT results in novel genetic recombination on which selection can act, with potential outcomes including HT displacing one or both parental species, and expansion of HT genotypes with greater ecological amplitude into areas previously uninvaded by toadflax. This could result in increasing difficulty in managing HT with currently available chemical and biological controls (Sing et al. 2016), which increases the importance of early detection and implementation of appropriate management of HT populations.

To maximize effective control strategies, resource managers benefit from environmental suitability maps that predict the distribution of invading species. These maps are a product of ecological niche modeling (also known as species distribution modeling or bioclimatic envelope modeling). Ongoing advancements in geographic information systems (GIS) and greater availability of modeling algorithms and detailed geospatial environmental data, including remote sensing data, have led to the use of ecological niche modeling for numerous applications in ecological research (Peterson et al. 2011; Jarnevich et al. 2015). Modeling aids assessment of future areas of invasion because requisite data can be obtained relatively quickly and models have also been shown to accurately predict future invasion areas (Jarnevich et al. 2010; Koncki and Aronson 2015). Ecological niche models empirically relate species occurrence data and environmental variables to create environmental suitability maps for a defined area (Bradley et al. 2012; Rauber et al. 2016). These models also identify the most significant environmental conditions contributing to the distribution of a species. Early detection of infestations is more effective when supported by knowledge of conditions that promote species invasions (Bradley and Marvin 2011).

MaxEnt modeling uses a machine-learning method to calculate the distribution of maximum entropy and estimate the probability of species presence throughout a delineated study area (Philips et al. 2006). It is notably well suited for species with a small number of occurrence records, as with HT in this study (Benito et al. 2009; Lopez-Alvarez et al. 2015), due to its regularization procedure that prevents over-fitting such models (Phillips et al. 2006; Hernandez et al. 2006). MaxEnt is the most commonly used ecological niche modeling application for inferring species distributions, niches, and environmental tolerances (Warren and Seifert 2011).

This research used MaxEnt modeling plus GIS processing to identify areas vulnerable to toadflax invasion in Montana, Wyoming, and Colorado. The objectives were to: 1) identify the most important contributing environmental variables associated with Dalmatian, yellow, and hybrid toadflax distributions; 2) create environmental suitability maps for these three toadflax taxa; 3) create an overlay and a hot spot map predicting areas most at risk for hybrid toadflax occurrence; and 4) compare two modeling approaches by measuring the degree of agreement between the hybrid toadflax environmental suitability map and the overlay prediction map.

Materials and Methods

Study Area. Our study area consisted of the states of Montana, Wyoming, and Colorado, selected to provide a sample of DT and YT occurrence data across a region of management interest. Geographic features of the study area include the western Continental Divide traversing the Rocky Mountains. This mountain range encompasses significant elevation differences and geographic variation, driving considerable variation in local climatic conditions. East of the range are plains regions in all three states, characterized by lower elevations, higher mean temperatures, and a longer growing season (WRCC 2016). Elevation in the study area ranges from 550 – 4400 m (1800 to 14,433 feet), contributing to a heterogeneous climate. The clay content in soils also varies – approximately 5% in northwestern Montana up to nearly 60% east of the Rockies, also in Montana (SoilGrids 2017). Across the area, clay content is typically lower in the mountains and higher at lower elevations. Annual precipitation is heterogeneous throughout the three-state area as well, ranging from highs of approximately 290 cm in the mountains to lows of less than 14 cm in southwestern Wyoming and southcentral Colorado (ClimateWNA 2017). The most prevalent land uses and land cover in our study area are

coniferous forest, grazed rangelands, farming, and developed urban locations, representing a broad array of ecosystems and plant communities (USDA 2012).

Toadflax Occurrence Data. Occurrence data for YT, DT and HT were obtained from seven online herbaria accessed between November 22 and December 13, 2016: Rocky Mountain Herbarium (<https://www-lib.uwyo.edu/digitalherbaria/index.php>), SEINet (<http://swbiodiversity.org/seinet/collections/download/index.php>), Consortium of Pacific Northwest Herbaria (<http://www.pnwherbaria.org/>), Global Biodiversity Information Facility (www.gbif.org), Early Detection and Distribution Mapping System (<http://www.eddmaps.org/>), University of Colorado (<http://www.colorado.edu/cumuseum/research-collections/botany-section-university-herbarium-colo>), and iDigBio (<http://www.idigbio.org>). Occurrence data were also provided by individual contributors ranging from county weed managers to federal agency regional managers throughout the three-state area. Twenty individuals contributed occurrence data for DT and 18 for YT, but only three for HT, indicative of low levels of recognition of the hybrid taxon and likely less knowledge of its prevalence (occurrence maps for each taxon provided as Supplemental Figures 1, 2, and 3).

After acquiring occurrence data for all taxa, we executed a spatial filtering step to reduce spatial autocorrelation (Brown 2014). Filtering methods outperform unfiltered methods in correcting for sampling bias, which increases spatial autocorrelation and may lead to overfit models with falsely high-performance values (Boria et al. 2014). The spatial filtering step was performed using the “Spatially Rarefy Occurrence Data” tool in SDMtoolbox (Brown 2014) in ArcGIS 10.2 (<http://www.esri.com/arcgis/>). This step eliminated duplicate points clustered within a radius, which was set to 3 km, to prevent statistically over-weighting a clustered region.

When filtering was complete, 1024 points remained for DT, 1159 for YT, and 32 for HT; these occurrence data were inputs for the subsequent modeling process.

Occurrence location bias was addressed by creating a bias layer using the “Gaussian Kernel Density” tool in SDMtoolbox (Brown 2014). The bias layer down-weights the importance of occurrence points in areas with a greater number of samples (Elith et al. 2010). This corrects for potential sampling bias and mitigates clumping resulting from more prevalent occurrence data from areas that are of greater botanical interest or exposed to more human activity. For example, our original data set included multiple reports of toadflax occurrence for the Greater Yellowstone Area and the Colorado Front Range, but dropped because they were known to be associated with increased human observation in these two areas, compared to other parts of our study area.

Environmental Variables. Based on the biological and ecological characteristics of toadflax described above, we evaluated 73 environmental variables in the form of geographic information system (GIS) layers as possible distribution predictors (Table 1). These variables are categorized by climate, land use and land cover, phenology metrics, soils, topography, and remote-sensing-derived vegetation indices. The spatial resolution for all GIS layers was 1 km² and Albers Equal Area Conic was the coordinate system used. Some layers required resampling to conform to 1 km² spatial resolution (Supplemental Table 1).

We downloaded and processed climate data using ClimateWNA (Climate Western North America) v5.30 (Wang et al. 2012; <http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/>). Decadal, seasonal and annual data for 1991 – 2000 and 2001 – 2010 were obtained for the study area. An R script was created to average the two decadal layers for each variable to generate twenty-year mean layers. Consideration of 47 climatic variables increases

the accuracy of the final model relative to other common approaches (e.g. the 19 PRISM BioClim variables).

We then incorporated a land use and land cover layer for 2011 from the National Land Cover Database provided by the Multi-Resolution Land Characteristics Consortium (Homer et al. 2015). This national layer was clipped to our study area following recommended protocols (http://www.mrlc.gov/faq_lc.php).

The phenology metrics and the vegetation drought response index (VegDRI) were downloaded from the United States Geological Survey (USGS) Earth Explorer web application (<http://earthexplorer.usgs.gov/>). These data are collected from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on the National Aeronautics and Space Administration (NASA) Terra Satellite. VegDRI weekly data were downloaded for 2010 – 2015; phenology metrics annual data were downloaded for 2010 – 2014 (2015 data were unavailable when modeling was performed). We calculated the mean and standard deviation layers for the VegDRI and phenology metrics layers. The annual data were used to create multiyear mean and standard deviation layers. For example, the five years of VegDRI mean layers were averaged into a single layer representing the multiyear mean.

Soils data were downloaded from the World Soil Information site in the SoilGrids collection (SoilGrids 2017). Clay percentage at depths of 0-5 cm and 5-15 cm were used as variables in modeling.

We then used Earth Explorer to download the Global 30 Arc-Second Elevation GTOPO30 Digital Elevation Model (DEM) product (<https://lta.cr.usgs.gov/GTOPO30>). These data were analyzed in ArcGIS 10.2 to create layers for slope and aspect. The Euclidean distance

from water layer was constructed from this DEM and vector water body data for the study area obtained from Earth Explorer (<http://earthexplorer.usgs.gov/>).

Lastly, we retrieved the normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) products (MOD13A3 Vegetation Indices Monthly 1km) from the online MODIS Re-projection Tool (<https://mrtweb.cr.usgs.gov/>). These products were obtained for each month from 2010 to 2015. The NDVI and EVI data were handled in the same manner as the phenology and VegDRI data, to create multiyear mean and standard deviation layers.

Ecological Niche Modeling and Environmental Suitability Maps. Given its improved performance in predicting potential distributions compared to other modeling techniques (Philips and Dudik 2008), we chose Maximum Entropy Modeling or MaxEnt (version 3.3.3k; <https://www.cs.princeton.edu/~schapire/maxent/>; Phillips et al. 2006) to create environmental suitability maps. The entire MaxEnt modeling process was performed once for each toadflax taxon.

The variable selection process was performed incrementally using layers from each group of environmental variables to determine which layers significantly contributed to taxon-specific predicted distributions. The “jackknife” and “response curve” outputs of MaxEnt, along with knowledge of the taxon’s biology, were used to rank the importance of each variable to the respective model. After cross-correlations were assessed between environmental variables only one variable from each group of highly correlated variables was retained (Pearson correlation coefficient $|r| \geq 0.75$) in the go-forward models (Lestina et al. 2016). After variable(s) with the most significant contribution to the model from one group were identified, we added the next group of variables. The determination process was repeated until the highest-contributing

variables for the current group were found, then the next group was added, and so on until the final suite of variables was selected (Table 2).

Models were averaged across 10 replicates using the 10-fold cross-validation procedure in MaxEnt. We evaluated model performance using the area under the receiver operating characteristic curve (AUC). AUC measures the probability that a random presence point in the study area is ranked above background (or pseudo-absence) points (Philips et al. 2008). The AUC value is a common metric to assess MaxEnt models, with the benchmark value of 0.8 representing a highly accurate model. We also assessed our models by comparing 0% and 10% training presence test omission rates. A zero percent omission rate indicates that all the training presence locations were found within the predicted suitable environment, with 10% omission rates indicating that 10% of training presence locations lie beyond the predicted taxon-specific suitable environment (Liu et al. 2013). The default settings in MaxEnt do not always produce the best predictions (Merow et al. 2013; Kumar et al. 2014); accordingly, MaxEnt was executed with varying feature types and regularization multipliers (specifically, 1, 1.5, 2, 2.5, and 3). We calculated the Akaike's information criterion (corrected for small sample size: AICc) using environmental niche modeling tools or ENMTools (Warren et al. 2010). AICc values were determined for models with various settings to select the model with optimal features and regularization multiplier as the final model (Supplemental Tables 2, 3, 4).

Predicting Hybrid Occurrence. We used two different modeling approaches to predict HT environmental suitability: first, the HT MaxEnt model based on environmental parameters for currently known HT locations, and second, a map overlay of predicted DT and YT distributions used to predict hybridization zones. The HT MaxEnt model was created with the inputs of taxon occurrence data and candidate environmental variables – the same method used for predicting

the DT and YT environmental suitability. The results of this method were then compared with overlay results. The MaxEnt model output had a threshold applied to produce a binary map – areas where HT is and is not expected. For the overlay map, the process involved the following steps, with the first two steps performed for both DT and YT. First, in ArcGIS we converted the final average ASCII file created by MaxEnt into a grid raster with the “ASCII to Raster” tool. Second, we reclassified these grid rasters to threshold classification maps, using the “10 percentile training presence logistic threshold” from MaxEnt results (Carter and Young 2011). The values used for this threshold from MaxEnt outputs were: DT = 0.4722 and YT = 0.4762. This classification results in an area that encompasses the probability of the 90% most accurate occurrence points. This step reduced the environmental suitability map to two classifications – suitable and unsuitable. Third, we added the classification maps together using the “Raster Calculator” tool. The resultant map contained four values describing the environment as: 1) unsuitable for both taxa 2) suitable for DT only 3) suitable for YT only and 4) suitable for both taxa and therefore suitable for HT. This overlay approach stems from the biological assumption that co-invasion of DT and YT is the best predictor for HT occurrence.

Completion of these steps made it possible to generate a hot spots map for HT using classified areas with a threshold applied for: 1) the MaxEnt HT environmental suitability map, applying the same threshold variable with value for HT of 0.2771, and 2) the overlay map. The HT hot spots map shows classes of suitability for these two areas as well as the combined area, i.e., where both the MaxEnt and overlay map predicted HT suitability.

Statistical Analysis. A principal component analysis (PCA) of extracted data was performed to discriminate DT and YT in environmental space (Green 1971; Austin and Smith 1989). An R script was used (Broennimann et al. 2012) to generate a graphical depiction of environmental-

space overlap. To evaluate the similarity of quantity and similarity of locations between the HT MaxEnt environmental suitability binary map (i.e. threshold applied to give values of 0 or 1) and the HT zone of the overlay map, we used the Kappa statistic tool in the Map Comparison Kit (Visser and de Nijs 2006; West et al. 2016).

Handling Uncertainty in Modeling. Uncertainties arise from various sources when utilizing presence-only or presence-background modeling techniques to predict environmental suitability for a species, including sampling bias, spatial autocorrelation, multicollinearity between environmental variables, temporal resolution of data, and modeling techniques (Guisan et al. 2007a,b; Veloz 2009; Syfert et al. 2013). We addressed sampling bias prior to modeling using the “Gaussian Kernel Density of Sampling Locations” tool in SDMtoolbox to create a bias file which facilitates control of background point selection. However, sampling bias in the field may also occur when HT infestations are incorrectly reported as DT; this is an easy mistake to make (S Sing, personal observation). Rarefying presence points addressed spatial autocorrelations to the limit used (i.e., 3km). Multicollinearity between environmental variables was handled throughout the modeling process by producing the correlations table and evaluating highly correlated variables during variable selection. The climatic variables were derived from decadal averages from the ClimateWNA application for the years of 1991-2010, though occurrence data ranged from 1913 to 2016. The temporal differences between these datasets causes uncertainties as the climatic conditions may not accurately represent the conditions that toadflax populations experienced when they were surveyed (Lestina et al. 2016). Assessing the risk of toadflax invasion may be perceived as limited with the modeling techniques we used; such a limitation could be overcome by ensemble modeling.

Results and Discussion

Model Performance. Model assessments fell into three categories: area under the receiver operating characteristic curve (AUC), principal component analysis, and the Kappa statistic. Our AUC metrics were all near the benchmark: DT 0.762, YT 0.810, and HT 0.853 (Table 2). Model selection was based on the AICc process that identified MaxEnt settings yielding the optimal level of complexity when considering the biology of each taxon and environmental suitability predictions (see Tables 2, 3, and 4). The PCA showed significant overlap of the environmental envelopes of DT and YT (Supplemental Figure 4). This aligns well with the commonalities in environmental variables, as discussed below. When comparing the predicted hot spots for HT occurrence, between the HT environmental suitability binary map and the HT zone of the overlay map (Supplemental Figure 5) the Kappa statistic was 0.261, implying a low degree of similarity. This emphasizes the importance of using more than one modeling approach for an emerging taxon such as HT where few occurrence points are known. Mapped results are consistent with known biological and ecological characteristics of the three toadflax taxa, except for one area in northeast Wyoming which is discussed below.

Environmental Variables. The top three environmental variables (Table 3) contributing to the DT model were summer mean maximum temperature (25.7% relative contribution to the MaxEnt mathematical model), elevation (25.4%), and land use and land cover (16.7%).

Originating from the dry climate of the Mediterranean, DT prefers warm summer temperatures with mean daytime highs ranging from 22 to 32° C based on model results. The model also showed that DT favors elevations below 2800 m, where temperatures are warmer. DT overwinters above ground as a vegetative rosette, which potentially restricts it to lower elevations where it is not exposed to extreme winter cold. Regarding land use and land cover, DT

was modeled as most likely to occur in open vegetated areas dominated by grasses, and areas that had reduced vegetation but with more roads or other human-created disturbances, which may reflect the level of disturbance favored to facilitate invasion. For YT, the most significant environmental variables were autumn (September – November) mean maximum temperature (24.7%), land use and land cover (21.3%), and mean NDVI (20.6%). YT flowers and continues growing later in the year than DT and is best suited to sites with mid-range autumn temperatures similar to those found in its native range of temperate Eurasia (in our study area, mean daytime highs of 8 – 20° C according to the model). Unlike DT, YT overwinters below ground, allowing it to survive colder winter temperatures at higher elevations than DT. YT also adapts to a greater diversity of land cover types than DT, ranging from grassy areas to those with more roads or human-created disturbances than DT, consistent with its invaded range throughout nearly all North America. Higher mean NDVI is associated with YT occurrence, possibly because abiotic conditions that will make vegetation greener, notably higher moisture, are preferred by YT. Lastly, for HT, we found number of frost-free days throughout the growing season (47.1%), end-of-season NDVI (22.2%), and summer (June – August) precipitation (17.6%) to be the highest contributing environmental variables to the model. Given that the hybrid may combine ecophysiological and phenological traits from both parental taxa (Turner 2012) it is possible that like DT it favors sites with warm summers, and like YT, where it can exploit higher summer precipitation and a later growing season.

Predicted Invasive Ranges for Dalmatian Toadflax and Yellow Toadflax. The MaxEnt model-generated environmental suitability map for DT predicts large areas of western Montana, northwestern and eastern Wyoming, and the northeastern plus lower elevation parts of the Western Slope and Front Range of Colorado as suitable environment (Figure 1). These coincide

with lower elevation areas with higher temperatures, as enumerated by the significant environmental variables. For YT, suitable habitat was identified in western Montana, northwestern and southeastern Wyoming, and Colorado west of the Front Range (Figure 1). Areas with higher elevations, higher moisture, and lower temperatures are shown as more suitable for YT, also in line with our predictive YT environmental variables.

The model identified several areas as suitable habitat for both DT and YT, though occurrence data for these locations were sparse or lacking (see Supplemental Figures 1 and 2 for mapped occurrence points). These areas included the Black Hills region in northeast Wyoming, the southwest corner of Wyoming west of the Red Desert, and large parts of northwestern Colorado. Either YT and DT occur more widely in these areas but have been under-reported (presence), these toadflaxes have yet to spread extensively (absence), or the modeling methods were incorrect. The possibilities of greater parental species occurrence or lack of spread should be considered by managers as they identify at-risk areas for toadflax establishment and survey these areas accordingly.

Predicted Invasive Range for Hybrid Toadflax. As described earlier, we used two different modeling approaches to predict the invasive range for HT within our study area. The overlay map (Figure 2) combines the results of the DT and YT environmental suitability maps to identify areas at risk for HT. This approach assumes that HT invasion is driven by co-occurrence of DT and YT, with subsequent gene flow between them and formation of a hybrid zone. Invasion predictions based on the overlay map therefore exclude the possibility of HT introduction via seed movement from an established HT population elsewhere. A further limitation of the overlay map is that it is based on the threshold values to produce binary suitability throughout the study area; in fact, habitat suitability is more accurately considered as a continuum and therefore the

overlay rendering represents a generalization. However, for the purposes of our modeling, constructing the overlay is informative despite these limitations as it identifies areas where co-occurrence of the parental taxa and generation of novel HT populations is likely. The overlay map in Figure 2 highlights these at-risk areas. They include large parts of western Montana; in Wyoming the Black Hills region, the Laramie and Medicine Bow mountain ranges and the foothills of the Big Horn and Wind River mountain ranges; and in Colorado the Front Range and much of the Western Slope.

As an alternative modeling approach, we used MaxEnt to generate an environmental suitability map for HT using locations of known HT populations and associated environmental variables. The resulting map (Figure 2) predicts more limited HT occurrence than the overlay map, with approximately half the study area identified as being of low environmental suitability. This is likely the result of the low number of occurrence points ($n=32$) used to generate the environmental suitability map. With fewer occurrence points, a smaller climatic and environmental range is deemed hospitable, and the HT environmental suitability map in Figure 2 should therefore be considered a conservative, or short term, prediction. The area modeled as suitable HT environment includes several national parks, wilderness areas and Native American reservations (Supplemental Figure 6). These present management challenges discussed below.

Figure 2 also shows much of central Montana and part of north central Wyoming identified by the model as suitable habitat for HT, even though neither parental taxon has been reported there; these regions are mapped in yellow in Figure 3. Heavier clay soils in north central Wyoming could make this region inhospitable for toadflax (J Sutton, Grouse Mountain Environmental Consultants, personal communication). However, genetic recombination can expand the ecological amplitude of novel hybrids beyond that of either parental species (Milne

and Abbott 2000; Turner 2012), potentially allowing HT populations to invade a wider range of environments than YT or DT. The following scenarios could result in HT establishment in an area where neither parental species is found: transport of HT seed by biotic (wildlife, livestock or birds) or abiotic (water, wind) agents; progenitor elimination by a biocontrol or herbicide ineffective on the hybrid, allowing HT to persist alone; or HT establishment via heterosis (i.e. hybrid vigor) resulting in its spread, dominance and displacement of YT and DT. The potential for such HT establishment should raise a red flag for managers because an HT expansion in such an area presents the challenge of recognizing and controlling HT before it becomes less feasible to eradicate.

The overlay map and the environmental suitability map have predicted areas of HT occurrence in common (Figure 2). This shows strength in either approach, and that the MaxEnt model for HT performed well despite the low number of occurrence points available for model input. By combining the two model outputs we can most accurately visualize the predicted areas of HT occurrence common to both models: Figure 3 shows these areas in red. These are hot spots at high risk of HT invasion as predicted by both the HT environmental suitability map and the overlay map. The highest risk areas are western Montana, the Black Hills region, the Laramie Range in southeast Wyoming, plus the Front Range and parts of the Western Slope of Colorado. It is possible to generate a hot spots map for a smaller area, such as a county, within the three states; however, doing so requires rerunning the modeling step using test data and environmental variables only from that area to prevent potential loss of reliability and prediction accuracy (Kumar et al. 2014). The potential toadflax distributions could be altered by projected climate change for the study area, and this subject is a candidate for future research.

Based on identified hot spots, field crews may be able to identify and treat HT invasions; though investigations of herbicide and biocontrol treatments for HT are ongoing, results are preliminary so management recommendations are still pending. Herbicide treatments are however often a last resort option in national parks, wilderness areas, and on Native American reservations (Supplemental Figure 6) where options for their use and application can be delayed or obstructed by public relations or regulatory issues. Two species of stem-boring weevils – *Mecinus janthiniformis* Tosevski & Caldara, and *Mecinus heydenii* Wencker – attack HT under greenhouse conditions (S Sing, personal observation) but field impact is so far unknown. Successful biocontrol or herbicide treatments on DT and YT in the presence of HT may select for resistant HT by eliminating the parental species, hence the need for ongoing research to identify effective HT-specific chemical and biological controls. The risk of unchecked HT spread becomes increasingly elevated if HT is unaffected by control measures and no longer subjected to competition with its progenitors.

Our results provide weed and land managers insight into favorable conditions and predicted environmental suitability and distributions for three invasive toadflax taxa in the U.S. Northern Rockies. This is the first study of the potential geographic distribution of HT, which appears to be the most aggressive invader among these three weedy toadflax taxa (Turner 2012). We aim to raise awareness among managers about the risks associated with HT and the areas in which high priority needs to be given to controlling invasive toadflax. Identifying areas of hybrid-only invasion in the field could lead to greater understanding of the conditions enabling such invasions to establish and persist. With that knowledge, managers and field crews may have a higher awareness of where to find HT and to plan early detection and rapid response programs

accordingly. The emergence of invasive hybrid plants will remain an ongoing phenomenon – one that weed and land managers can better control with the aid of modeled suitability predictions.

Tables

Table 1. Name and description for environmental variables selected to model environmental suitability for Dalmatian, yellow, and hybrid toadflax in Montana, Wyoming, and Colorado. A seasonal variable is suffixed by * and implies four variables – winter, spring, summer, and autumn.

Variable	Description	Variable	Description
Climate			
MAT	Mean annual temperature (°C)	MWMT	Mean warmest month temperature (°C)
MCMT	Mean coldest month temperature (°C)	TD	Temperature difference between MWMT and MCMT, or continentality (°C)
NFFD	The number of frost-free days	FFP	Frost-free period
bFFP	The day of the year on which FFP begins	eFFP	The day of the year on which FFP ends
Tave*	Seasonal mean temperature (°C)	Tmax*	Seasonal mean maximum temperature (°C)
Tmin*	Seasonal mean minimum temperature (°C)	DD_0*	Seasonal degree-days below 0°C
DD18*	Seasonal degree-days above 18°C	NFFD*	Seasonal number of frost-free days
MAP	Mean annual precipitation (mm)	MSP	Mean annual summer (May to Sept.) precipitation (mm)
AHM	Annual heat-moisture index	SHM	Summer heat-moisture index

PAS	Precipitation as snow (mm) between August in previ year and July in current year	Eref	Hargreaves reference evaporation (mm)
CMD	Hargreaves climatic moisture deficit (mm)	PPT*	Seasonal precipitation (mm)
PAS*	Winter and spring precipitation as snow (mm)	MAR	Mean annual solar radiation (MJ m ⁻² d ⁻¹)
RH	Mean annual relative humidity (%)		

Land use and land cover

luc	Land use and land cover
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Phenology metrics

AMP	Amplitude - Maximum increase in canopy photosynthetic activity above the baseline (scaled NDVI).	EOSN	End of Season NDVI - Level of photosynthetic activity at the end of measurable photosynthesis (NDVI value).
MAXN	Maximum NDVI - Maximum level of photosynthetic activity in the canopy (NDVI value).	SOSN	Start of Season NDVI - Level of photosynthetic activity at the beginning of measurable photosynthesis (NDVI value).

TIN Time-Integrated NDVI - Canopy photosynthetic activity across the entire growing season (interpolated NDVI).

Soils

%clay_0-5cm	Proportion of clay in the soil at 0-5 cm depth	%clay_5-15cm	Proportion of clay in the soil at 5-15 cm depth
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Topography

slope	The percent slope of each cell	aspect	The compass direction (in degrees) the slope faces in each cell
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Euclidean distance to water

Straight-line distance from a cell to a water source

Vegetation Indices

NDVI	Mean of NDVI data for 2010 - 2015	NDVI SD	Standard deviation of NDVI data for 2010 - 2015
EVI	Mean of EVI data for 2010 - 2015	EVI SD	Standard deviation of EVI data for 2010 - 2015
VegDRI	Mean of the annual means of VegDRI data from 2010 – 2015	VegDRI SD	Standard deviation of the VegDRI data from 2010 – 2015

Table 2. Summary of final ecological niche models for Dalmatian (DT), yellow (YT), and hybrid toadflax (HT).

Model	Model Description			MaxEnt Settings*		Model Evaluation		
	No. of occurrence data points	Most significant environmental variables	No. of variables	Features	β	Average test AUC	Minimum training presence test omission	10 percentile training presence test omission
DT	1024	max summer temp., elevation, land use/cover, continentality, NDVI [^] mean, % clay 5-15cm, winter ppt., annual heat-moisture index	8	LQTH	2	0.762	0.002	0.1186
YT	1159	max autumn temp., land use/cover, NDVI mean, winter ppt., % clay 5-15cm, summer degree days above 18°C, slope	7	LQTH	1.5	0.810	0.0026	0.1209
HT	32	summer number of frost free days, end of season NDVI std. dev., summer ppt., slope	4	LQH	1.5	0.853	0.0667	0.1

*MaxEnt settings are linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) features; β is the regularization multiplier;

AUC is area under the received characteristic curve; [^]NDVI is normalized difference vegetation index.

Table 3. Percent contribution of environmental variables to each MaxEnt model.

Dalmatian toadflax model variable	Percent Contribution	Yellow toadflax model variable	Percent Contribution	Hybrid toadflax model variable	Percent Contribution
Max. summer temp.	25.7	Max. autumn temp.	24.7	Summer number of frost free days	47.1
Elevation	25.4	Land use/cover	21.3	End of season NDVI std. dev.	22.2
Land use/cover	16.7	NDVI mean	20.6	Summer precip.	17.6
Continentality	11.8	Winter precip.	16	Slope	13.1
NDVI mean	9.1	% clay 5-15cm	11.4		
% clay 5-15cm	4.6	Summer degree days above 18°C	3.3		
Winter precip.	3.4	Slope	2.7		
Annual heat-moisture index	3.3				

^NDVI is normalized difference vegetation index

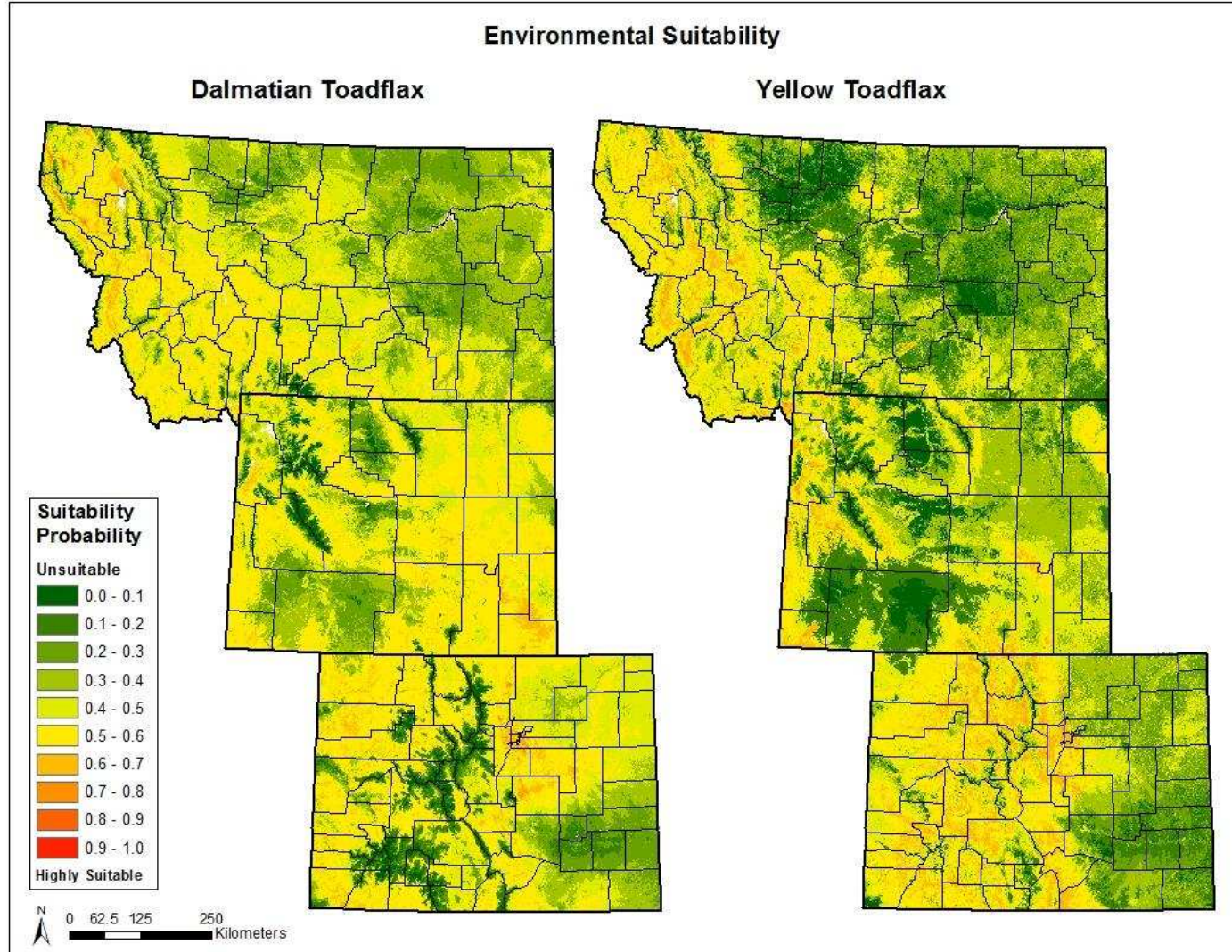


Figure 1. Environmental suitability maps indicating predicted suitability based on occurrence data and most significant environmental variables as modeled in MaxEnt; suitability categories are given as the probability that Dalmatian toadflax or yellow toadflax would grow in the indicated locations.

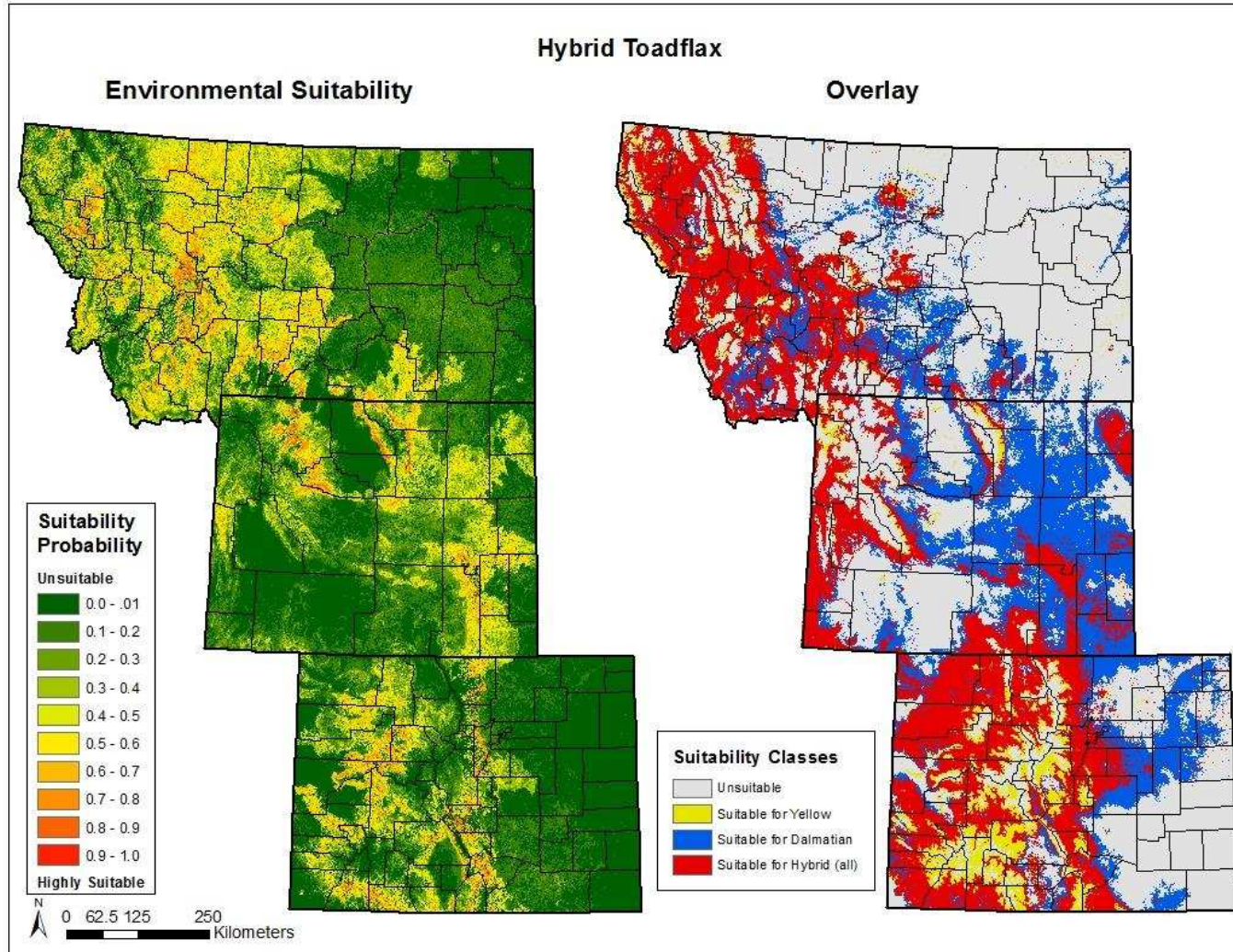


Figure 2. Environmental suitability maps indicating predicted suitability based on occurrence data and most significant environmental variables as modeled in MaxEnt; suitability categories are given as the probability that hybrid toadflax would grow in the indicated locations. On the right are regions of overlap of Dalmatian and yellow toadflax, showing where their hybrid is more likely to occur as both parental species may exist there.

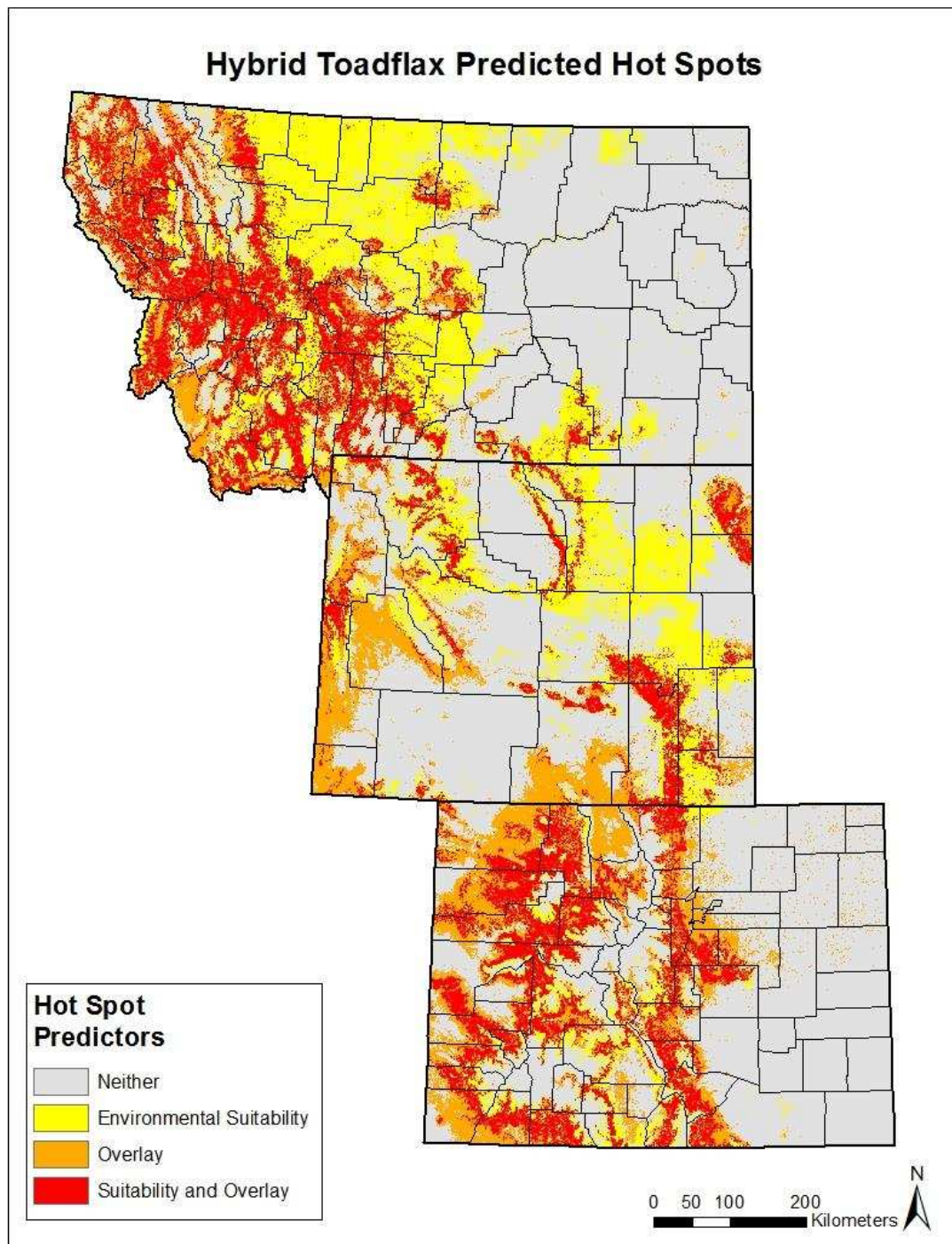


Figure 3. Potential hybridization regions indicated in red – areas predicted as most suitable by the hybrid toadflax environmental suitability map and the overlay map. As the hot spots result from both prediction methods, they represent the highest risk areas for HT predicted by this research.

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Chapter Three: Interviews with Weed and Land Managers

Introduction

To solicit feedback on the environmental suitability, overlay, and hot spots maps, seven people involved with toadflax management were interviewed. More specifically, the purposes of the interviews were to inquire about the accuracy of the maps, seek reactions to the hybrid toadflax maps, understand the pros and cons of such predictions, and query for a level of awareness of the invasive potential of hybrid toadflax. The interviewees were chosen out of the 20 individuals that contributed toadflax occurrence data used in this modeling project as they expressed interest in being involved with subsequent research activities. Only one of these people was a stakeholder in the full thesis research project; the other six were interviewed for their unique perspectives based on their professional roles and the regions in which they work. Interviewees came from all three states in the study area (Montana, Wyoming, and Colorado) and included two US Forest Service employees, one county extension representative/weed coordinator/teacher, one extension representative with a rangeland focus, two state weed specialists, and a project manager in environmental consulting. A document was emailed to each participant that described the generation process and the specific context of each map (Maps are found in Chapter 2 and identified by figure number below). Interviews were conducted via phone March 20–31, 2017. The identity of respondents will remain anonymous. All three taxa were covered by the discussion questions – Dalmatian toadflax (DT), yellow toadflax (YT), and hybrid toadflax (HT).

Other relevant published work. No published studies were found where modelers asked managers for feedback on ecological niche model output. A relevant, though conservation focused, paper about integrating modeling with decision making is reviewed here. Villero et al.

(2016) discussed recommendations to improve the results of conservation processes by incorporating modeling into decision making, with focus given to spatial products. In contrast with my interviews, their paper described results of stakeholder integration throughout a research project, whereas I sought to learn perspectives of several non-stakeholders with end results in hand, perhaps a unique approach for soliciting feedback. Villero et al. (2016) used three best-practice successful example projects to elaborate how to use models to identify the most suitable habitats for implementing conservation management actions, with each contributing to the emergent results. The authors concluded that predictive distribution maps can be suggestive of potential management actions, though they can be misunderstood and misused if modeling goals and uncertainties are not explained to decision makers. To mitigate such risks, they reported uncertainties with each modeling step, highlighted the correct interpretation and known limitations of model outputs, and made recommendations to stimulate use of model outputs. The authors also highlighted striving for consensus with targeted audiences throughout the project to guarantee acceptance of the final map products (Villero et al. 2016). Stakeholder feedback enables alignment of spatial products to specific information requirements to support successful decision making (Laurance et al. 2012). Realization of these processes is possible when multiple project stakeholders with common goals provide input throughout the course of the research.

Interview questions

The interview questions posed to each interviewee follow; everyone received all questions. Responses were typed during the interviews, and are discussed by theme in the subsequent sections of this chapter.

1. What is your reaction to the HT occurrence map [Supplemental Figure 3 – in chapter 2])?
2. Do you think the three environmental suitability maps (DT, YT, HT) are accurate based

- on your understanding of the presence of toadflax in the field [Figures 1 and 2]?
3. Do you have any questions about how the overlay map was created [Figure 2]? What's your reaction to it?
 4. What is your reaction to the hot spots map, which combines the HT environmental suitability map and the overlay map [Figure 3]?
 5. How would you use the information provided in these maps?
 6. How useful do you consider such predictive maps? What provides value to you from modeling geographic distributions like this? What opportunities for improvement do you see?
 7. Do you know or suspect you have HT on the lands you where you work/that you manage?
 8. Are you concerned about HT as a significant invasive problem? If so, how concerned and why? If not, why not?
 9. Would you like to share any additional thoughts?

Summary of Interview Responses

Extent of knowledge of hybrid toadflax. Most interviewees had either little or no knowledge about HT occurrence, identification, and biocontrol methods. "Occurrence of HT is underreported – nobody is looking that diligently for it," said one respondent. Another described how only one area in their managed lands is known to have an HT population, though they stated: "toadflax has been my nemesis – predominantly YT" and later added that toadflax is "pretty tough." Regarding identification, one interviewee said that their small field crew doing the scouting did not know how to identify HT – they are aware of the taxon and have seen pictures, but seeing it in the field would solidify their knowledge. Thoughts about biocontrol

efficacy on DT and YT were shared by two people: “The way biocontrols are spreading I don’t think of toadflax as much of a concern. I think HT will get the same level of management concern and treatment [as DT and YT] – unless HT goes off into new areas.” Secondly, a biocontrol project with DT that showed a 95% success rate was described, with the addition that “the potential for biocontrol of HT seems exciting.” The current state of herbicide and biocontrols is discussed in the section "Current research on hybrid toadflax control" below.

Perceptions of the environmental suitability, overlay, and hot spots maps. Five of seven interviewees stated that the DT and YT environmental suitability maps looked correct based on their knowledge of the species’ distributions. The sixth individual said that the DT map surely looked good, though they did not know what drives YT distribution and did not comment on the accuracy of the YT environmental suitability map. The seventh respondent considered the DT and YT maps inaccurate and cited a lack of occurrence data in the central and eastern part of Montana as the likely reason why. Six respondents did not comment on the accuracy of the HT environmental suitability map, likely because of limited knowledge of HT in the field. The single comment heard was “the HT suitability map is as expected, though perhaps there is more suitability in Wyoming like south of Jackson and the southwest area of the state.”

The DT and YT environmental suitability maps are used to create the overlay map, whose premise is coexistence of the parental species is the strongest driver for hybridization. The overlay map received one neutral response, one concerned with the formatting of the map itself, and five positive responses – those that deemed the map accurate and easy to read. “It gives more information than we have now,” said one interviewee, adding “it is good information to focus efforts for controlling HT.” “It is a good regional representation,” said another.

The hot spots map was created by combining the HT environmental suitability map with the area of predicted suitability for HT from the overlay map. Feedback on the hot spots map varied, with valuable insights coming from neutral or negative responses (e.g., those pointing out where the map was inaccurate). One interviewee said the map predicted suitability in south Campbell County, Wyoming, which is in fact unsuitable for YT due to the area being arid and having clay soils. Another respondent liked the map, though he thought more suitability would show up in southwest Wyoming. A positive response was that “[the hot spots map] looks pretty accurate, it includes the places where I’d expect HT to show up.” Lastly, an individual stated that the predicted distribution of HT in the hot spots map was “kind of alarming.”

Concerns about HT distribution. Three interviewees knew they have HT on the lands where they work, one suspected they have more HT than currently identified, another suspected they have HT, and three do not know, or could not determine, if HT exists in areas they oversee. Another noted that given their knowledge of DT and YT, there is a definite potential for HT to be a management problem. “I think there is a lot more HT out there than captured in these maps,” said one interviewee, adding “I initially thought HT [populations] were very localized – now when I go to any site with DT, I’m likely to find HT.” Lastly, the respondent commented how DT is becoming less abundant in their area and HT is getting more abundant.

Heterosis, i.e. “hybrid vigor”, was described as a likely contributor to the expanding distribution of HT. “HT is tougher than its parents, and I know DT and YT are tough in themselves” said one individual. Another interviewee described several factors contributing to their concerns: “both DT and YT are present in [my area] and I acknowledge the issue of hybrid vigor and resistance to control. Secondly, environmental conditions are changing and I don’t

think anyone has a good handle on these – not just climate, temperature and precipitation, but also land use and disturbance.”

Another respondent stated they had a low level of concern about HT spread. They know where DT and YT tend to invade and biocontrols have shown some good promise on these species, leading them to be “not too terribly concerned.” Further, they have not had difficulties with chemical controls on DT and YT, though “we never really know about HT with herbicides.” Lastly, they noted their level of concern was dependent on the forthcoming research results of biocontrol and herbicide effectiveness on HT, as well as the outcomes from these interviews.

Concerns about HT management. The ability to successfully manage HT was a common concern among those interviewed. “The parents are already a challenge to manage... HT may be more of a challenge. We will essentially be selecting for HT if we successfully control DT and YT [in a community with HT] because HT will propagate if controls fail on it.” Another interviewee said “the most difficult management issue is that it’s so resilient, like YT. HT commonly requires extra time and effort to get to it and control it.” According to a subject matter expert, the research on control effectiveness on HT is still in progress “at this time, we can’t make any management recommendations [about controls]. This will become a problem when people spray HT without results.” “I worry that we don’t pay enough attention to [noxious weeds] – funding and management efforts are insufficient. Aspects of this include inventory, monitoring, management, and controls” stated an interviewee about the bigger picture challenges with noxious weeds. “In the scheme of noxious weed management there are too many invasives that are and are not listed. Competing resources arise in funding, politics, and fiscal resources” said one manager. Another respondent stated “[management] priorities can change if nastier weeds show up and resources are limited.” Two people stated the results of our research could be

used to request more resources, either by lobbying for more budget or helping to convince folks that toadflax is a genuine threat.

Usefulness of maps and increasing awareness. Five of seven interviewees described the set of maps as useful; the other two said the maps would be more useful with the ability to zoom in or have a county-level view (further discussed in the section “Limitations and opportunities associated with this modeling research” below). Three respondents stated that the maps could raise awareness among weed and land managers, and one noted that following on from heightened manager awareness, increased field crew alertness to HT would be a likely outcome.

Targeting prioritized locations. The topic of prioritizing HT management received a spectrum of responses. Two people mentioned that targeting locations based on the maps was either an initial or non-important step – that HT-aware field crews can look for the taxon on the ground and their findings become more important than the predictive maps. However, the ability to “narrow down the search for HT where it hasn’t been reported yet” and “focus efforts of control according to predictions such as targeting hybrid hot spots” was important to two others. One respondent stated “an ideal outcome would be focusing funds of management efforts – getting the biggest bang for the buck from high-risk areas.” The ability to prioritize likely travel vectors, for example, interstate traffic and traffic from a neighboring state, was important to one individual who said that “the maps are nice to show where toadflax is coming from and the areas that are most susceptible.” Targeted outreach was also discussed – selecting specific counties or communities for outreach and ignoring others, such as those where HT environmental suitability was notably low.

Current research on hybrid toadflax control. As mentioned previously, research on herbicide and biocontrol treatments for HT was ongoing at the time of these interviews (March 2017). The

subject matter expert on this research described the investigation status as follows: A formal garden-based study comparing herbicide efficacy on DT, YT and HT was initiated in September 2016 to characterize toadflax genotype response to chemical management. Two species of stem-boring weevils – *Mecinus janthiniformis* and *Mecinus heydenii* – have been shown to attack HT under greenhouse conditions, but field impact is unknown. Herbicide and biocontrol investigations are ongoing and results are still preliminary, so management recommendations are pending (as of July 2017).

Limitations and opportunities associated with this modeling research

Inability to zoom in (e.g. to a county-level map). The capability to generate a county-level map or to zoom in from the three-state view was of interest to six of seven interviewees. Ecological and technical limitations presented by this are discussed in the “My Reflections” section below. This need came from several interviewees differing perspectives: where to and not to survey/intensify efforts; to provide field workers with a more detailed map for taxon location; and to increase value for instruction/outreach, during which people want to recognize their county or they may not grasp the importance of the map’s meaning to the specific lands they own and/or manage.

Incomplete occurrence data. The accuracy of our modeling results depends on comprehensive occurrence data for all three taxa, and it is difficult to capture a highly representative sample across a three-state region. Four interviewees had questions about sparse toadflax occurrence data at specific locations in their area (Supplemental Figures 1 – 3). These included Sweetgrass County, Montana, eastern Montana for DT and YT, the northeast corner of Colorado for YT, and Unita County, Montana for DT and YT. The effect of this missing data on the modeling (both environmental variable selection and all maps) could be that suitable areas for a taxon were left

out of the results. Such an area would need to be notably different than others that were deemed suitable by MaxEnt. This determination of suitability is only made for environments where the taxon is present. MaxEnt classifies all environmentally consistent areas with a similar probability of presence, thus the necessity for uniqueness in such an area.

Enhanced modeling. Several recommendations were made of ways that the modeling process could be improved; however, none of these are possible with the current MaxEnt software application. Other modeling applications may provide some of these capabilities, though it was beyond the scope of this research to investigate additional applications. The first recommendation was to have the model remove land cover areas of heavy coniferous forests where toadflax does not grow. MaxEnt is designed to handle land cover as a categorical variable – a single environmental layer describing many categories of cover such that all types are considered together. If no occurrence points existed in the coniferous forest cover type, then MaxEnt would exclude that category out of land cover; however, in processing other favorable environmental variables, the coniferous areas may end up being identified as suitable. Thus, MaxEnt does not perform a black-and-white exclusion of one category such as coniferous forest. The second recommendation was to define absence points – locations where toadflax is known to not exist – and incorporate those into the predictions. Other modeling applications include this function, e.g. generalized linear modeling (GLM), though care must be taken to not include ‘false’ absences (where a species was not detected during occurrence data collection; Hirzel et al. 2002). This could be particularly challenging over a multistate area and a multiyear period. The third recommendation was to factor in sites of herbicide application or biocontrol release, which could be implemented by a model as an area of decreasing probability of occurrence. The fourth recommendation was to input pollinator density data, and thereby describe a mutualism that may

lead to greater toadflax spread. Interspecific interactions are widely varied and introduce significant complexity to modeling, such that this suggestion may be the most difficult to address. The fifth recommendation was to predict toadflax potential population densities, which would be a very useful accompaniment to probability of occurrence (that MaxEnt currently generates) as it provides additional information that is important to management. The final recommendation was to show the predicted distributions over time (e.g., 5 to 10 years in the future) plus with or without treatment. MaxEnt can generate models using forecasted environmental variables such as climate at future dates, though doing so requires running the full modeling process.

Conclusions

The most important conclusion reached from these interviews was that nearly all respondents knew little about HT; a clear gap exists between awareness and occurrence of hybrid toadflax. However, most people acknowledged it as a considerable invasive threat based on the invasive capacity of the parental species and the potential distribution of HT. The maps shared with the interviewees were largely accepted for their accuracy in predicting suitable environments, other than minor exceptions. An interesting spectrum of responses was heard about the usefulness, benefits, and drawbacks of these predictions. Some found them highly useful and would target management in high-risk areas; others would not perform targeted management based on the maps. Benefits also come from increasing alertness of more weed and land managers plus field crews. The predominant drawback was the three-state extent of all maps – interviewees wanted an ability to zoom in on their lands of interest (further discussed in the next section). Conducting these interviews made a fulfilling and tangible contribution of sharing

knowledge about all three toadflax taxa among those directly involved with managing these invasive plants.

My Reflections

As the primary researcher, I was very happy to have the opportunity to talk with people directly involved with toadflax management about the predictive map products. These discussions bridged the gap between my research results and the application of predictive maps in the ‘real world’. I learned a lot from people’s unexpected comments; the feedback received was most insightful regarding awareness, county-level maps, and modeling enhancements.

It was quite clear from the discussions that the highest value provided by the maps was raising awareness – mainly in weed and land managers, also in field crews as well as those deciding on budgets for invasive plant control efforts. I think that by spreading the word, both with my interviews and the publication of the modeling results as a peer-reviewed journal article, recipients will tune in to the results of the HT controls research. Ideally, weed managers who need to know how to control HT will be made aware of the most effective herbicide and/or biocontrol treatments based on these research efforts. The goal here is to increase alertness and preparedness for field crews to control HT on their managed lands. If additional resources are required for control efforts to be successful, the maps produced were described as one way to justify such a need, according to one interviewee. This is a very fulfilling outcome of the research – increasing awareness among those interviewed, or those that contributed occurrence data, and potentially a wider group of people involved with managing and treating toadflax. The concerns raised about competing priorities in invasive species management for funding and other resources are acknowledged and understood. However, I hope my research results may lead to an appropriate level of prioritization of toadflax management, particularly hybrid toadflax.

With six out of seven interviewees requesting a county-level view or an ability to zoom in on the maps, it was very evident that there is an opportunity for maps that can guide localized control efforts. It was good to hear the desire to have this localized information to help address the threat of toadflax spread – managers want to control these invasives as well as possible. The rationale behind not being able to extract a county-level map from my results is that the accuracy level does not translate from the three-state area to a smaller area such as a county. To generate a county-level map with valid accuracy would require occurrence data solely from that county to train and test the model for a particular toadflax taxon. Additionally, environmental variables would need to be matched to the county-level extent, and may change based on the smaller scale. Thus, the MaxEnt modeling process would have to be repeated to correctly identify significant variables. County-level maps can be created, though they would require that the modeler work with occurrence points and environmental variable selection for an individual county.

Lastly, most suggestions for improved modeling addressed ways to make the model closer to what is seen in nature. Three comments were made about subtracting an element – land cover type, known absence of taxon, and previously treated locations, and one was made about adding an element – pollinator densities. It is insightful to understand the needs of those applying model results to on-the-ground efforts because they are above and beyond what the MaxEnt modeling application currently does. These needs constitute ways MaxEnt and/or other applications can be enhanced for realism from the perspective of those looking to apply the results to management efforts.

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Summary

The results on DT, YT, and HT in the U.S. Northern Rockies included identification of favorable environmental variables, predicted environmental suitability maps and – for HT – the overlay and hot spots distribution predictions. HT appears to be the most vigorous invader of these three taxa, and this is the first study of its potential geographic range. Hybridization hot spots were predicted for western Montana; northwestern, northeastern, and southeastern Wyoming; and the Western Slope and Front Range of Colorado. Model results also suggested that HT would have greater ecological amplitude than DT and YT – the hybrid may spread beyond the presence of its progenitors, specifically in north central Montana. The methods used for modeling HT as an emerging hybrid taxon with few recorded occurrence data serve as an example for other researchers of three different approaches to predict a hybrid's ecological niche. With our modeling results in hand, I interviewed seven people involved with managing invasive toadflax and learned that nearly all respondents knew little about HT. However, most people acknowledged the highly invasive capacity of DT and YT, and therefore considered HT a formidable invasive threat. With many invasive plants on managers' radar and limited resources, the objectives of this outreach evolved into raising awareness of the hybrid's potential distribution and informing interviewees about ongoing controls research. Six of the seven respondents wanted the ability to zoom in on the maps, for example to a county-level view (which is ecologically infeasible due to accuracy not transferring across geographic extents). This localized perspective would better facilitate targeting management in the highest priority areas, a capability manager need due to resource limitations and the necessity of highly effective treatment plans. The greatest outcome of this research was raising awareness about HT – its occurrence, the predicted geographic distribution, and the current state of herbicide and

biocontrol investigations. With this increased awareness, managers of weedy toadflax in the U.S. Northern Rockies will be better able to create scouting and treatment programs for emerging hybrid toadflax.

Limitations and Future Research

The ecological niche models presented here are limited based on the nature of the modeling applications and the data used. Several restrictions imposed by current models prevent addressing such aspects as interspecies interactions, for example, biocontrols or pollinators, predicting species population densities, and modeling environmental stochasticity. Additional pertinent limitations could be overcome; specifically, including absence points, removing land cover areas such as heavy coniferous forests, and predicting species distributions in future climate change scenarios. These gaps could be filled by using a different modeling application such as generalized linear modeling (for absence data) or different data with MaxEnt (for land cover and climate change). To research toadflax distribution under predicted climate change scenarios, existing literature can be consulted, notably for finding future climate data and MaxEnt modeling methods.

A significant unanswered ecological question following on from this research is: Does HT have a greater ecological amplitude than its parental species? To further investigate this question, a controlled experimental transplant of all three taxa could be conducted in two areas predicted suitable only for HT, that is, within north central Montana. Two areas are required to test independence of location and of isolated conditions. The null hypothesis is that all three taxa would survive and spread well; the alternative hypothesis is that DT and YT would not persist and only HT would. If HT demonstrates increased ecological amplitude, understanding the biotic and abiotic characteristics of the ecosystem could be insightful to further predict where the

hybrid may spread. Having more occurrence data for HT would similarly improve the prediction, though the accumulation of data likely will come from many contributors working in the field over time. The following questions represent research in progress: Is HT more invasive than YT or DT– does it spread faster and is it a better competitor in different environments? Does HT displace its parental taxa in an invaded area? Preliminary evidence suggests that HT can outcompete and replace both parental species.

Unanswered questions about outreach include: Which toadflax management outreach programs are currently more effective than others and why? Using HT as an emerging invasive plant in the study area could serve as a model taxon to investigate outreach effectiveness. Before this research can begin, management recommendations need to be finalized based on herbicide and biocontrol investigations. Then metrics for HT awareness could be defined and measured among managers before and after the various outreach programs are performed. Examples of such metrics include the knowledge of HT existence, how to identify HT, and the locations of currently infested areas. Measuring the treatment of HT in response to outreach would not be a good metric as it is confounded by resource limitations. Given these limitations and open questions, opportunities abound for future research on hybrid toadflax and associated outreach activities in the U.S. Northern Rockies and beyond.

Appendix

Supplemental Table 1. Summary of raster environmental variables, sources, and resolutions used in modeling.

Environmental		Original
Variables	Source	Resolution
Climate	ClimateWNA	1 km
Land use/cover	Multi-Resolution Land Characteristics Consortium (MRLC) National Land Cover Database 2011	30 m
eMODIS	USGS Earth Explorer	250 m
Phenology metrics		
Clay % at 0-5 cm,	ISRIC - World Soil Information SoilGrids	1 km
Clay % at 5-15 cm,	Collection	
Elevation	USGS Earth Explorer Global 30 Arc-Second Elevation GTOPO30 DEM product	830 m
Aspect, slope	Derived from GTOPO30 DEM	830 m
EVI, NDVI	USGS, NASA; Land Processes Distributed Active Archive Center; MRTWeb	250 m
VegDRI	USGS Earth Explorer	1 km

Supplemental Table 2. Summary of Dalmatian toadflax model selection using AICc. See Table 1 for variables' full names. Models are shown in order of decreasing number of parameters. The final model with moderate complexity is made bold. The AUC value is calculated from a single run, i.e. without ten-fold cross validation, so the value for model rank 1 (0.773) does not equal that in Table 2.

Variables	MaxEnt settings*	No. of variables	No. of parameters	AICc	Δ AICc	AUC	Model rank
tmax_sm, dem, luc, td, ndvi_m, clyppt_15, ppt_wt, ahm	LQTH, $\beta=1$	8	79	27229.7	-66.9	0.779	9
tmax_sm, dem, luc, td, ndvi_m, clyppt_15, ppt_wt, ahm	LQTH, $\beta=1.5$	8	63	27263.2	-33.4	0.773	8
tmax_sm, dem, luc, td, ndvi_m, clyppt_15, ppt_wt, ahm	LQH, $\beta=2$	8	58	27322.0	25.4	0.776	6
tmax_sm, dem, luc, td, ndvi_m, clyppt_15, ppt_wt, ahm	LQTH, $\beta=2$	8	56	27296.6	0.0	0.773	1
tmax_sm, dem, luc, td, ndvi_m, clyppt_15, ppt_wt, ahm	LQPH, $\beta=2$	8	52	27304.9	8.3	0.767	3
tmax_sm, dem, luc, td, ndvi_m, clyppt_15, ppt_wt, ahm	LQTH, $\beta=2.5$	8	51	27329.5	32.9	0.772	7

tmax_sm, dem, luc, td, ndvi_m, clyppt_15,							
ppt_wt, ahm	LQPTH, $\beta=2$	8	51	27284.9	-11.8	0.763	4
tmax_sm, dem, luc, td, ndvi_m, clyppt_15,							
ppt_wt	LQTH, $\beta=2$	7	49	27279.8	-16.8	0.774	5
tmax_sm, dem, luc, td, ndvi_m, clyppt_15	LQTH, $\beta=2$	6	49	27289.4	-7.2	0.783	2
tmax_sm, dem, luc, td, ndvi_m	LQTH, $\beta=2$	5	45	27424.1	127.5	0.757	10
tmax_sm, dem, luc, td	LQTH, $\beta=2$	4	35	27483.5	186.8	0.746	11

MaxEnt settings are linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) features; β is the regularization multiplier.

Supplemental Table 3. Summary of yellow toadflax model selection using AICc. See Table 1 for variables' full names. Models are shown in order of decreasing number of parameters. The final model with moderate complexity is made bold. The AUC value is calculated from a single run, i.e. without ten-fold cross validation, so the value for model rank 1 (0.817) does not equal that in Table 2.

Variables	MaxEnt settings	No. of variables	No. of parameters	AICc	Δ AICc	Test AUC	Model rank
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15, dd18_sm, slope	LQTH, $\beta=1$	7	72	30195.0	-28.4	0.819	6
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15, dd18_sm, slope	LQPTH, $\beta=1.5$	7	57	30208.3	-15.1	0.816	3
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15, dd18_sm, slope	LQTH, $\beta=1.5$	7	56	30223.4	0.0	0.817	1
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15, dd18_sm, slope	LQPH, $\beta=1.5$	7	55	30253.1	29.7	0.814	7
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15, dd18_sm, slope	LQH, $\beta=1.5$	7	49	30247.8	24.5	0.816	5
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15, dd18_sm, slope	LQTH, $\beta=2$	7	47	30247.6	24.2	0.817	4

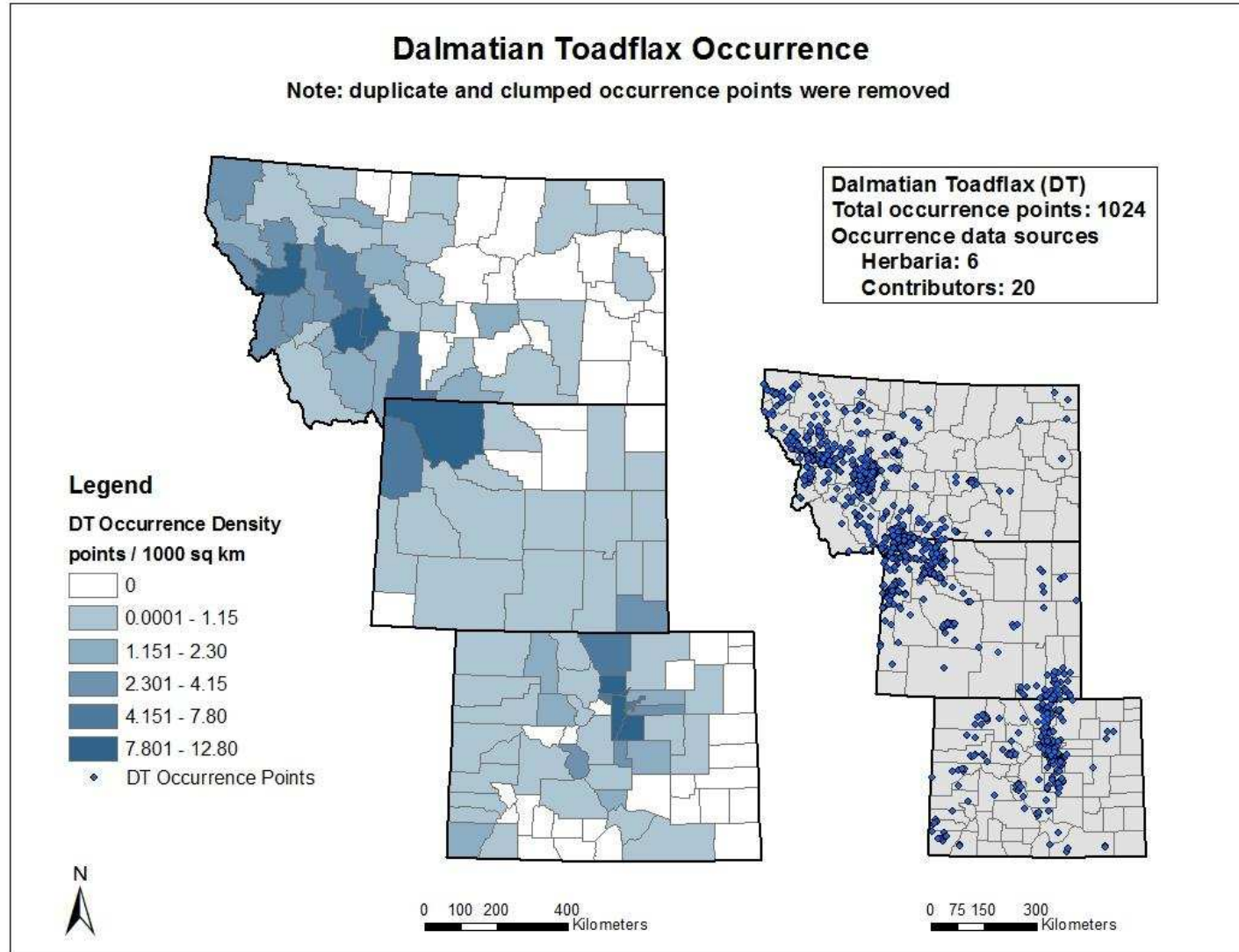
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15,	LQTH, $\beta=1.5$						
dd18_sm		6	47	30213.4	-10.0	0.816	2
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15	LQTH, $\beta=1.5$	5	46	30285.6	62.2	0.809	9
tmax_at, luc, ndvi_m, ppt_wt	LQTH, $\beta=1.5$	4	44	30624.7	401.3	0.786	10
tmax_at, luc, ndvi_m, ppt_wt, clyppt_15,	LQTH, $\beta=2.5$						
dd18_sm, slope		7	39	30277.8	54.4	0.816	8

MaxEnt settings are linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) features; β is the regularization multiplier.

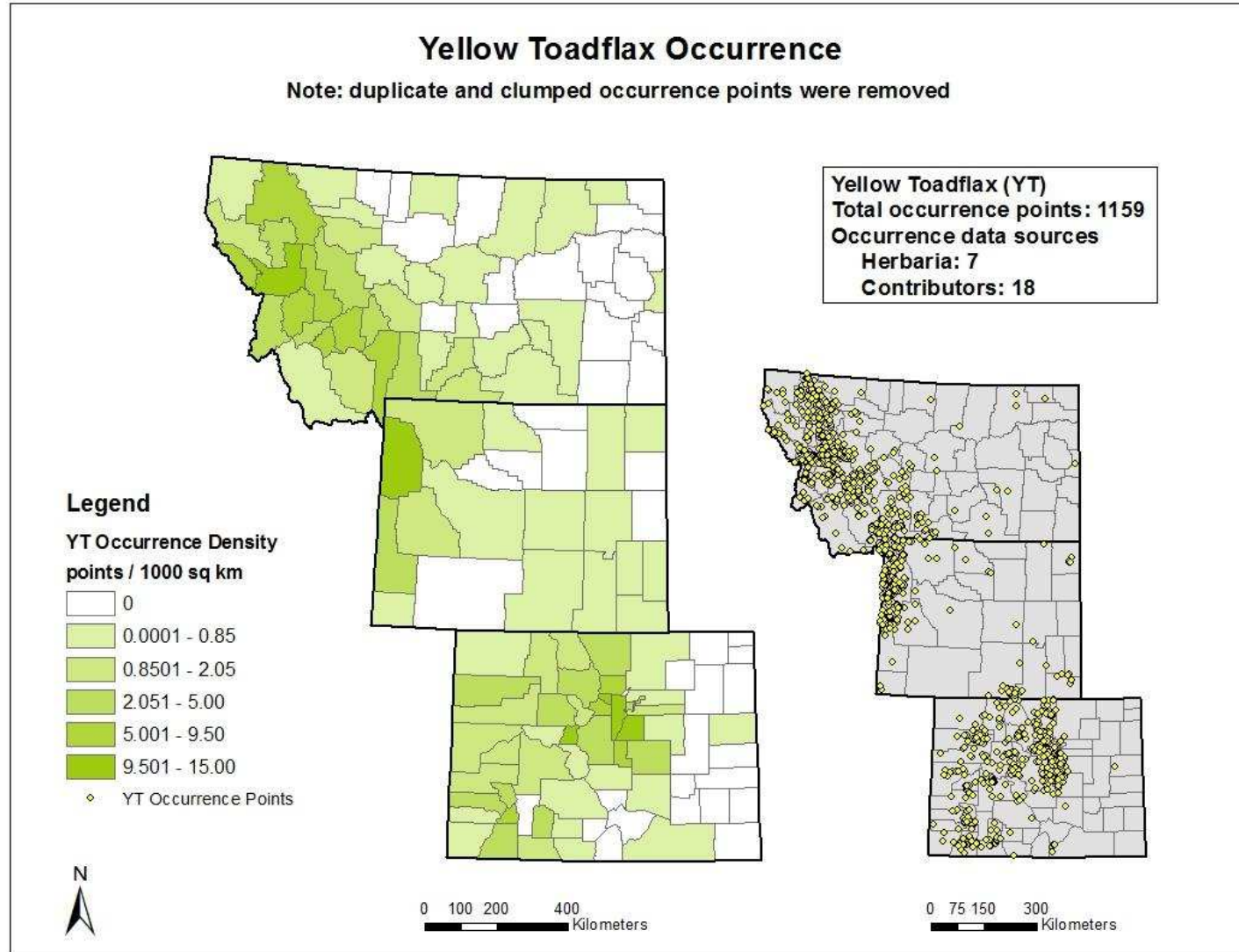
Supplemental Table 4. Summary of hybrid toadflax model selection using AICc. See Table 1 for variables' full names. Models are shown in order of decreasing number of parameters. The final model with moderate complexity is shown in bold.

Variables	MaxEnt settings	No. variables	Parameters	AICc	Δ AICc	AUC	Model rank
nffd_sm, eosn_sd, ppt_sm, slope	LQH, $\beta=1$	4	20	904.9	52.0	0.899	8
nffd_sm, eosn_sd, ppt_sm, slope	LQPH, $\beta=1.5$	4	19	896.8	43.9	0.895	7
nffd_sm, eosn_sd, ppt_sm, slope	LQPTH, $\beta=1.5$	4	16	860.4	7.5	0.904	3
nffd_sm, eosn_sd, ppt_sm, slope	LQTH, $\beta=1.5$	4	15	851.0	-1.9	0.9	2
nffd_sm, eosn_sd, ppt_sm, slope	LQH, $\beta=1.5$	4	15	852.9	0.0	0.895	1
nffd_sm, eosn_sd, ppt_sm, slope	LQH, $\beta=2$	4	13	843.6	-9.3	0.892	4
nffd_sm, eosn_sd, ppt_sm, slope	LQH, $\beta=2.5$	4	11	837.0	-15.9	0.889	6
nffd_sm, eosn_sd, ppt_sm	LQH, $\beta=1.5$	3	9	838.3	-14.6	0.873	5

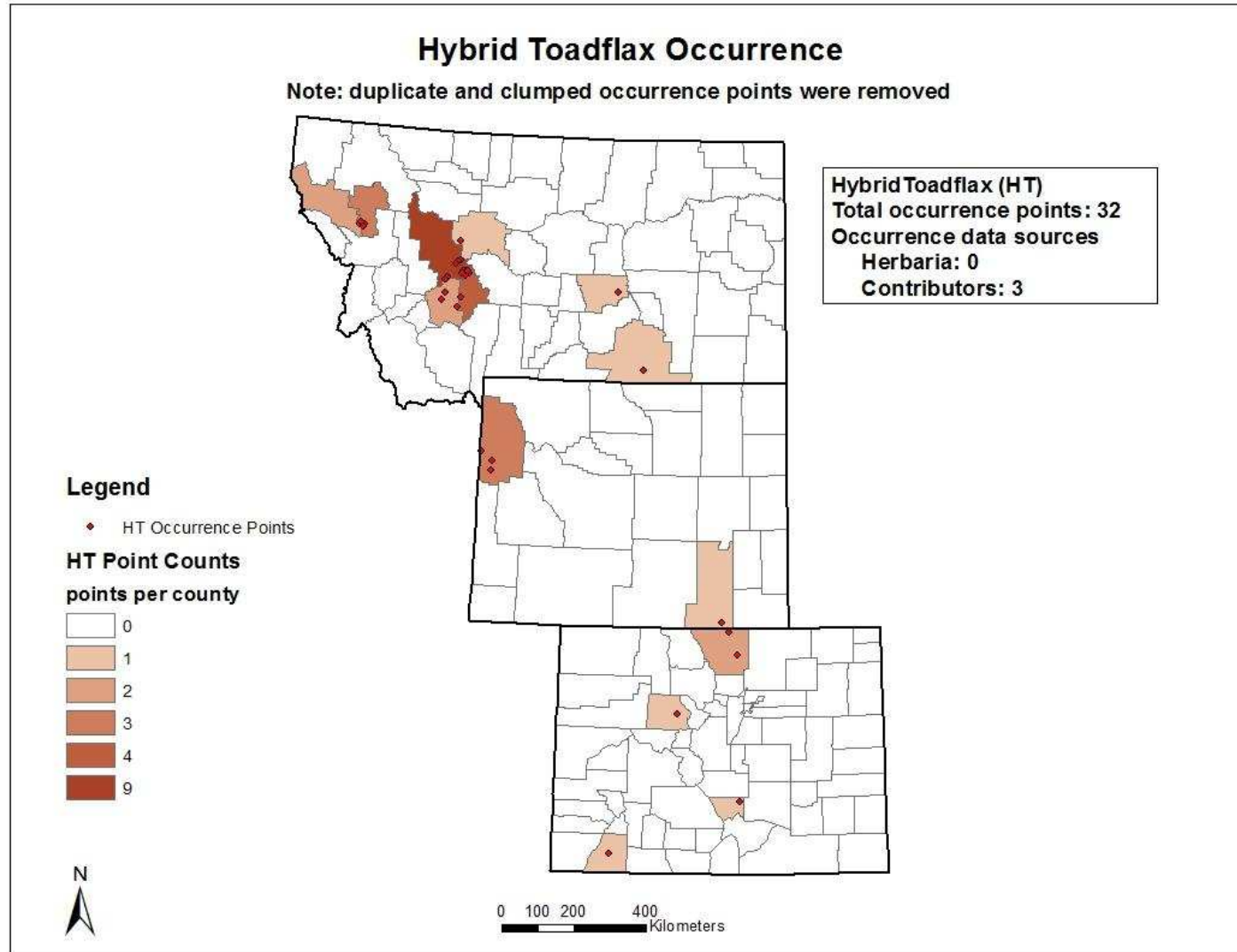
MaxEnt settings are linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) features; β is the regularization multiplier.



Supplemental Figure 1. Dalmatian toadflax occurrence shown graphically as points per 1000 square kilometers in each county of the study area and points of occurrence throughout the area. This map reflects where the taxon was recorded by an observer, which may imply some degree of sampling bias as not all areas were sampled equally.

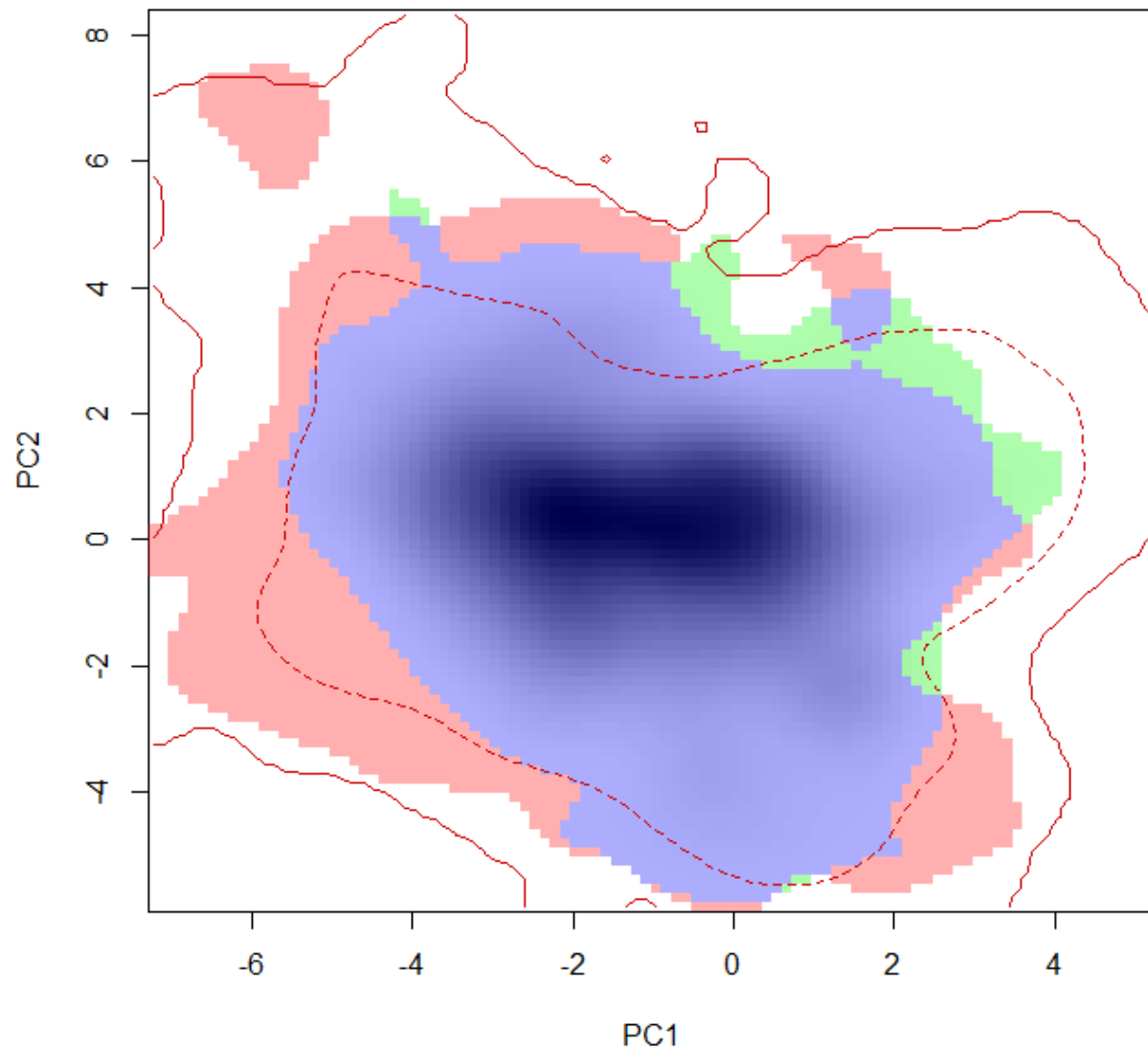


Supplemental Figure 2. Yellow toadflax occurrence shown graphically as points per 1000 square kilometers in each county of the study area and points of occurrence throughout the area. This map reflects where the taxon was recorded by an observer, which may imply some degree of sampling bias as not all areas were sampled equally.

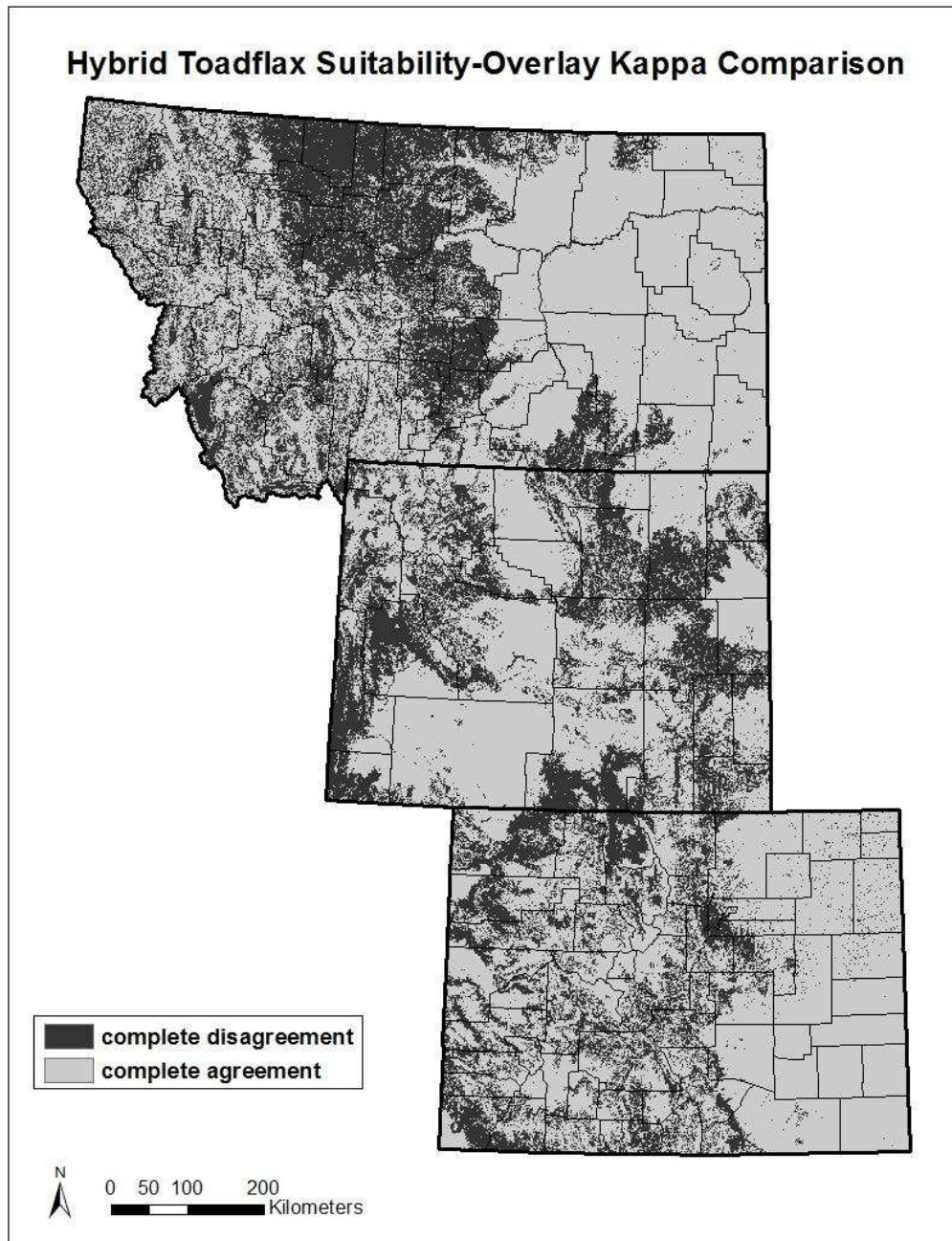


Supplemental Figure 3. In contrast to the maps for Dalmatian toadflax (Supplemental Figure 1) and yellow toadflax (Supplemental Figure 2), this map for hybrid toadflax occurrence shows the count of points per county instead of point density. Note the description of occurrence total points and data sources.

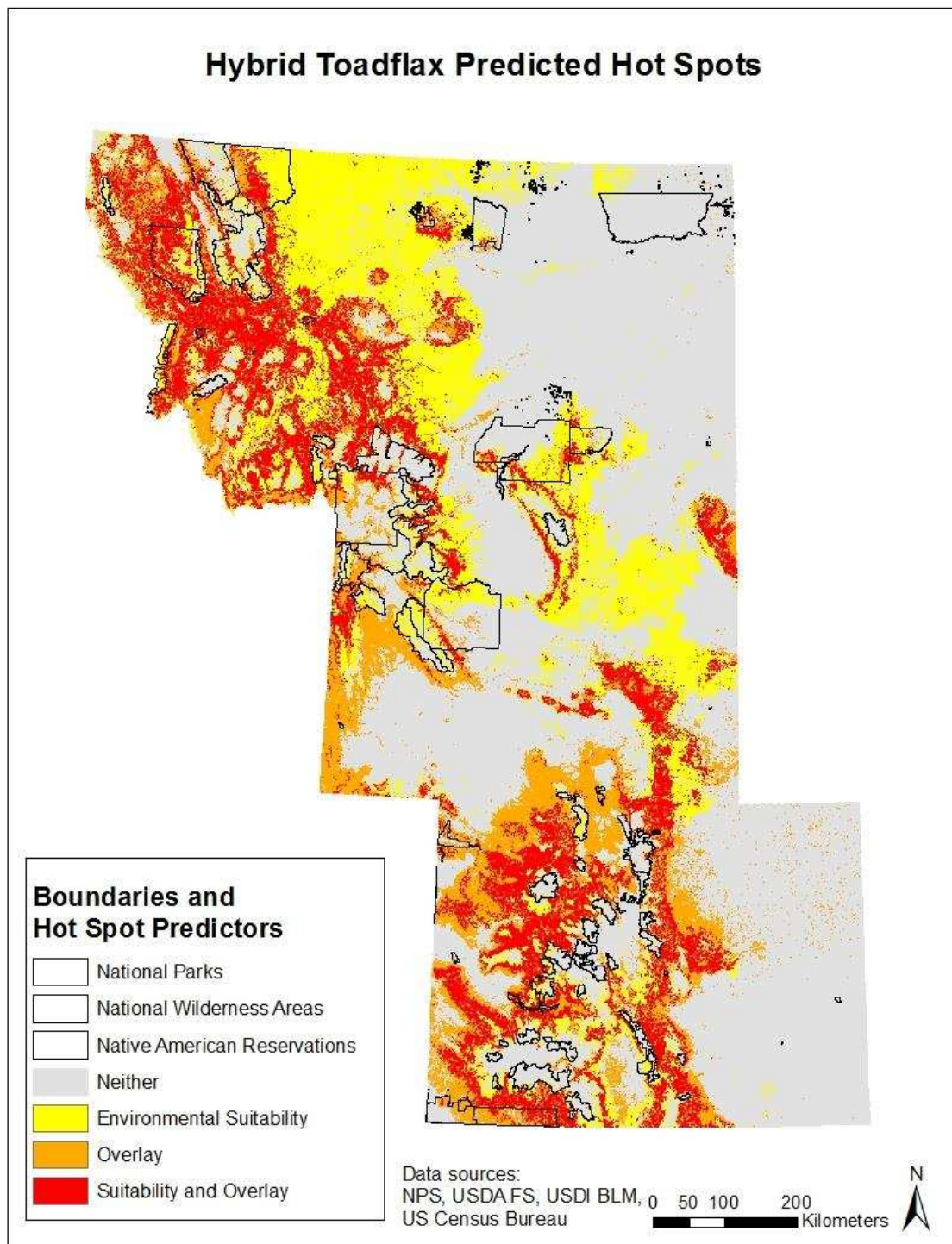
Dalmatian and Yellow Toadflax Niche Overlap



Supplemental Figure 4. Multivariate toadflax niche in MT, WY, and CO obtained with Principal Component Analysis (PCA). Red areas show the Dalmatian toadflax niche, green shows the yellow toadflax niche, and blue shows the niche overlap between the two taxa. Solid and dashed red contour lines show 100% and 75% of the environmental envelope for the study area, respectively.



Supplemental Figure 5. The graphical and statistical evaluation of similarity of quantity and similarity of locations between the hybrid toadflax environmental suitability threshold map (10 percentile training presence logistic threshold = 0.2771) and the hybrid toadflax zone of the overlay map. The low degree of similarity between the maps is reflected in the low value of the κ (Kappa) statistic, 0.261. This dissimilarity is likely caused by the hybrid toadflax environmental suitability map being generated from minimal occurrence data and being less accurate as a result.



Supplemental Figure 6. The hot spots map per Figure 3 is shown with national park, wilderness area, and Native American reservation boundaries. Note that the hot spot areas shown (in yellow, orange, and red) are identical to Figure 3.