Creating Invasive Plant Distribution Models for the Greater Yellowstone Ecosystem to Meet Conservation Objectives

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Authorization to Submit Thesis

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Abstract

The Greater Yellowstone Ecosystem (GYE) is a unique and intact ecosystem that covers over 8-million hectares across portions of Idaho, Wyoming, and Montana. The GYE has been protected through active management for conservation of lands, waters, and wildlife by the Greater Yellowstone Coalition (GYC) since 1983. The conservation goals of the GYC are currently challenged by invasive plants that reduce forage quality and plant diversity. Susceptibility models within geographic information systems (GIS) can effectively direct ground surveys to locate invasive plant populations when their special extent is small. Early detection of infestations less than one hectare are commonly eradicated. Once an infestation reaches 1,000 hectares it is unlikely to be eradicated, so ongoing containment costs will be necessary. Every dollar spent on prevention can avoid 17 dollars spent later for control which is why early detection is critical. The first chapter of this thesis details construction of new susceptibility models for meadow hawkweed (*Hieracium caespitosum* Dumort.) and orange hawkweed (*Hieracium aurantiacum* L.) in 1.31 million ha of the GYE using known locations of each species with aspect, slope, precipitation, and Sentinel-2 satellite spectral data. Models were used to select transect locations within susceptible areas for plant cover acquisition to identify indicator species and habitat types. Approximately 662,000 ha were determined to be susceptible to meadow hawkweed and 436,000 ha were determined to be susceptible to orange hawkweed, representing 51% and 33% of the study area, respectively. Forty-three 20-meter transects were surveyed; seven indicator species of meadow hawkweed and three indicator species of orange hawkweed (two of which were indicators of both) were identified. Transects were in 10 different habitat types within predicted orange or meadow hawkweed susceptibility. Eight habitat types were shared by both species but only meadow hawkweed was predicted in the big sagebrush/Idaho fescue type and only orange hawkweed was predicted in the Douglas-fir/common snowberry habitat type. The second chapter of this study extended susceptibility models created in Idaho, using Idaho presence data for leafy spurge (*Euphorbia esula* L.) and rush skeletonweed (*Chondrilla juncea* L.) into 1.12 million ha of the GYE. Model extension was used due to few known occurrences of leafy spurge or rush skeletonweed in the GYE that prevent creation of independent GYE models. The environmental variables used for these models were maximum and minimum temperature, sun angle, precipitation, and National Agriculture Imagery Program spectral data. Susceptibility was divided into low, moderate, and high categories (plus a not-susceptible category). Only 105,100 ha (9% of the study area) were predicted to be susceptible to leafy spurge. Rush skeletonweed susceptibility was predicted across 396,500 ha (33% of the study area). Overall, the study area was at a low risk to leafy spurge and rush skeletonweed invasions based on the extension of Idaho susceptibility models. When managing a region as large as the GYE, it is important to prioritize efforts on landscapes at the greatest risk to invasion because funds are often limited, and early detection is critical for successful eradication or control.

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Dedication

My parents have always been my biggest supporters and believed in me when I didn’t believe in myself. I am finally old enough to almost understand how incredibly vast their love is and that the good in my life is thanks to their steadfast devotion to letting me find my own path.

I cannot thank my husband, Clay, enough for moving to Idaho so I could pursue my passion. He has cooked and cleaned and listened to the ups and downs throughout this degree; for that, I am immensely grateful.

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Abstract

Habitat susceptibility models developed from remotely-sensed environmental data and known locations of a target species allows ground survey crews to locate the species of interest. Ground validation within the study area can reveal weaknesses of the model, leading to modifications, such as plant communities to exclude from consideration. Further, indicator species of potential presence of the target plant species can confirm to survey crews that they are searching within susceptible plant communities. An indicator species is typically associated with a specific habitat type and can be used as a surrogate for determining the presence of other, often less common, species. The objectives of this study were: 1) develop susceptibility models for meadow hawkweed (*Hieracium caespitosum* Dumort.) and orange hawkweed (*Hieracium aurantiacum* L.) using known locations and environmental data, 2) identify indicator species of orange and meadow hawkweed then assess their indicator power, 3) determine habitat types where these invasive hawkweeds might occur, 4) create susceptibility maps that can be served on platforms like ESRI's Collector application to allow mapping of invasive plant species on mobile devices. Susceptibility models were developed for orange and meadow hawkweed for 1.31 million ha of the Greater Yellowstone Ecosystem using documented locations of each hawkweed species and remotely-sensed environmental variables. Approximately 662,000 ha were determined to be susceptible to meadow hawkweed and over 436,000 ha were determined to be susceptible to orange hawkweed, representing 51% and 33% of the study area, respectively. Removing dense lodgepole pine areas from the models improved model fit based on error of commission (false positive) of dense lodgepole pine stands within hawkweed susceptibility. Error for dense lodgepole pine was reduced from 86% to 49% in the meadow hawkweed model and 100% to 9% in the orange hawkweed model. Plant cover data were collected along forty-three 20-meter transects within the susceptible range of orange and meadow hawkweeds. Plant community composition was assessed using a chi-squared contingency test and indicator power analysis. Meadow hawkweed had seven indicator species and orange hawkweed had three indicator species. There were 10 identified habitat types within predicted hawkweed susceptibility. Both meadow and orange hawkweed susceptibility overlapped in eight habitat types. Big sagebrush/Idaho fescue was only predicted to be susceptible to meadow hawkweed and Douglas-fir/common snowberry was only predicted to be susceptible to orange hawkweed. Understanding indicator species and habitat types associated with target invasive species complements susceptibility models when conducting field surveys by signifying suitable habitat to evaluate.

Introduction

Scientists have acknowledged negative impacts from weed presence for over a century (Shaw 1893). Aware even then that weed removal, although difficult, should occur promptly to reduce injury to desirable plants. Invasive plants, defined here as nonindigenous plants that have negative impacts on the systems where they occur, can reduce forage production, alter fire return intervals, reduce soil water content, and change native plant composition (Balch et al. 2013; Pfeiffer and Gorchov 2015). Invasive plants are a contributing factor in the decline of the federally threatened and endangered species (Nature Conservancy 1996). As of 2017, 566,600 ha of national parks were infested, with only 17,400 ha controlled (NPS 2019); land managers currently lack sufficient resources to meet the ecological threat. It is imperative to focus management efforts in areas with the greatest risk of invasion. Early detection of invasive plants when infestations are relatively small (i.e. <1,000 hectares), and meticulous eradication efforts can be the difference between efficient eradication and millions of dollars for ongoing control to stem biodiversity loss (Nature Conservancy 1996; Rejmánek and Pitcairn 2002).

The Greater Yellowstone Ecosystem (GYE) is a unique and intact ecosystem, spanning more than 8-million hectares across portions of Montana, Idaho, and Wyoming. It is characterized by a diverse flora with many vegetation types including conifer forests, sagebrush steppes, and mountain meadows (Despain 1990). The GYE has been protected by the Greater Yellowstone Coalition (GYC) through legislative and administrative action focused on keeping the ecosystem whole and minimizing disturbance. Invasive plants within the GYE challenge the conservation goals of the GYCC. When managing a region the size of the GYE it is important to prioritize efforts on landscapes at the greatest risk to invasion. Invasion can occur when propagules of invasive plants are present in an area that is susceptible to invasion (Wallace and Prather 2015). Susceptibility models accessed within geographic information systems (GIS) can efficiently direct ground survey efforts to locate invasive plant populations, saving land managers time and money.

Susceptibility modeling incorporates environmental factors that contribute to plant communities at a broad scale (Shafii et al. 2003; Lass et al. 2011). The first step to developing a susceptibility model is to identify abiotic and biotic factors (e.g. slope, aspect, elevation, vegetation indices), linked to the distribution of a target species; factors that identify a gradient where the target species is likely found (Lass et al. 2011). Abiotic conditions such as aspect and slope have a direct impact on solar radiation and moisture levels. In the northern hemisphere, south- (equatorial) facing aspects receive more sunlight than north- (polar) facing aspects so plants on equatorial facing slopes will likely show greater water stress (Holland and Steyn 1975). Moisture conditions influence plant communities. A study in Chile found that equatorial facing slopes had fewer species of evergreens than polar-, east-, and west-facing aspects (Armesto and Martínez 1987). Solar radiation also varies by sun slope angle. Solar radiation on equatorial-facing aspects increases as slope angle increase whereas polar-facing aspects receive less solar radiation as slope increases due to shading (Holland and Steyn 1975). Abiotic conditions directly impact biotic communities that can be interpreted using remote sensed data.

Multispectral reflectance data, imagery that includes multiple bands (images) of different wavelengths of light radiation (USDA 2017), can be used to interpret some biotic conditions remotely (Lass et al. 2011; John et al. 2018). The reflectance bands encompass visible light and near-infrared light; 4-band imagery is most commonly used in ecological studies: red, green, blue, and near-infrared (NIR) (Lass et al. 2011). Bands can be used independently or combined to calculate indices. The normalized difference vegetation index (NDVI; Tucker 1979) is widely used because it differentiates between dense, living vegetation and sparse or senesced vegetation (e.g Eitel et al. 2011; Lass et al. 2011).

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{Red}}{\mathrm{NIR} + \mathrm{Red}}$$

Recent studies have also incorporated the short-wave infrared band (SWIR, central λ=1610 μm) to calculate additional indices such as the normalized difference water index which relates to the plant water content (John et al. 2018). Reflectance data detect differences in

$$\mathrm{NDWI} = \frac{\mathrm{NIR} - \mathrm{SWIR}}{\mathrm{NIR} + \mathrm{SWIR}}$$

surface solar reflectance of land cover types because living vegetation reflects more NIR light than dead vegetation while dead vegetation reflects slightly more visible light (red, green, blue) than living vegetation. Surface water reflects less visible and only a fraction of the NIR light reflected by living plants (though dense conifer stands can look similar to water in blue light reflectance, due to scattering) (Jensen 2007). Rocks can reflect similar levels of visible light as living plants but have low NIR reflectance. Differences in visible and NIR light reflectance of living plants, dead plants, water, and rocks allows cover types to be differentiated.

Once key environmental factors are determined for a target species, the second step of model development is to digitize areas of known infestations of the target. GIS tools combine environmental factors at known infestations and predict areas likely to be invaded based on similar conditions (Shafii et al. 2003, 2004; Rew and Maxwell 2006). Areas that are most similar to the known infestations are considered to be highly susceptible to invasion of the target species. Areas that are highly different from the conditions at the known locations are considered to have low or no susceptibility to the invader.

Plant communities change through secondary succession and disturbance requiring periodic changes to models. Model predictions can be made when new locations of invasive plants are discovered and when updated GIS data are available. When conducting ground surveys, it is important to understand if a site is susceptible based on current site conditions. The absence of the target species is not enough to confirm whether the location is susceptible to invasion. Propagules may not have arrived yet or if propagules have arrived, their low abundance make detection difficult. Surrogate-based approaches may be used to estimate habitat susceptibility based on site conditions that can be evaluated on the ground, such as indicator species presence or current habitat conditions (Halme et al. 2008; Thuiller et al. 2012; Jones et al. 2018).

Habitat type is a term used to describe ecological characteristics of a location that act as a guide to distinguish between sites that can or cannot support certain plant species (Daubenmire 1984). Daubenmire (1984) mentions one important benefit to this method of describing habitats is that independent users can come to similar conclusions and adding useful information. Some scientists emphasize the climax community of a location, communities that exist after plant succession comes to equilibrium, others focus on the current community growing on a site (Despain 1990). A climax community may take decades or centuries to reach so an integrated approach of classifying habitat types allows invasion risk to be assessed based on the current conditions with some consideration of projected conditions.

Native and naturalized plant species with similar life-history characteristics of the target species may be considered an “indicator” of the potential presence of that target

(Fleishman et al. 2005). A reliable indicator species that is common and easy to identify can inform managers on the susceptibility risk when the target species is absent or in low abundance. Indicator species can also help identify habitat types that are susceptible to invasion.

The GYC's invasive species concerns include meadow hawkweed (*Hieracium caespitosum* Dumort. = *H. pratense* Tausch) and orange hawkweed (*H. aurantiacum* L.) because they are established within the GYE. Meadow hawkweed and orange hawkweed are among fifteen invasive *Hieracium* species that were introduced into North America as ornamentals from Europe, as early as the 19th century (Wilson 2007). Meadow and orange hawkweed are successful invaders due to high seed production and viability, long distance seed dispersal, and various methods of reproduction (Wilson and Callihan 1999; Wilson 2007). Meadow and orange hawkweed are apomictic, meaning they can produce seeds without fertilization (Tucker et al. 2003; León-Martíez and Vielle-Calzada 2019) and also reproduce via rhizomes and stolons (Wilson and Callihan 1999). Apomixis allows an individual plant to procreate without cross pollination which is especially advantageous when it is far from the source population. Hawkweed seeds are primarily wind-dispersed, but they can also be moved by animals. Once established, rhizomes and stolons allow plants to expand creating dense mats that can exclude other plants.

Meadow hawkweed is present in North America from British Columbia, Canada south to Oregon, USA and east to Wyoming; also, from Manitoba east to Newfoundland, Canada, and Minnesota east to Maine and south to Georgia, USA (Figure 1) (USDA, NRCS 2006). Vegetation types described in association with meadow hawkweed range from meadows to forests, and rocky outcrops to wetlands (Stone 2011). In Idaho, meadow hawkweed is found in prairies and mountain meadows (USDA NRCS/Shinn and Thill 2003). Meadow hawkweed is also found in forests and shrublands dominated by lodgepole pine (*Pinus contorta* Douglas ex Loudon), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), or Douglas hawthorn (*Crataegus douglasii* Lindl.) (Lass and Callihan 1997).

Orange hawkweed's distribution is broader than meadow hawkweed's distribution occurring in Alaska and across all southern Canadian provinces; it is also in the Northwest, Midwest, and Eastern United States (Figure 2) (USDA, NRCS 2006). Wilson and Callihan (1999) suggest that the sites most vulnerable to orange hawkweed within the Pacific

Northwest include: disturbed areas, roadsides, pastures, mountain meadows, logged areas, and abandoned farmland. Orange hawkweed is also known to occur in meadows used for commercial cranberry production (Jorgensen and Nauman 1994; Stone 2010). Orange hawkweed can be particularly troublesome because its pollen has allelopathic properties (Murphy and Aarssen 1995; Murphy 2001). Orange hawkweed pollen can lower fitness of other Asteraceae and Fabaceae species by reducing pollen germination, pollen tube development, and seed set (Wilson and Callihan 1999).

National strategies for managing aggressive, invasive plants incorporates prevention of new infestations, early detection and rapid response, control and management, and rehabilitation and restoration (Nature Conservancy 1996, USFS 2004). ESRI's Collector software application can be used to store and share GIS susceptibility models and map weed location data in the field (Esri, Redlands, CA). Further, maps depicting model derived susceptibility can be shared to other GIS platforms so the public can access weed data for independent research and map new weed locations.

This study aims to assist in early detection of meadow hawkweed and orange hawkweed in the GYE. The objectives were to: 1) develop susceptibility models for meadow hawkweed and orange hawkweed using known locations and environmental data, 2) identify indicator species of meadow and orange hawkweed then assess the indicator power, 3) determine habitat types where meadow and orange hawkweed occur, and 4) create susceptibility maps that can be served on platforms like ESRI’s Collector application to allow mapping of invasive plant species on mobile devices.

METHODS

STUDY AREA

The study area (Figure 1.3) encompasses Yellowstone National Park (YNP) and extends 38 km north and 13 km east of YNP (bounding coordinates: 111°15'36"W, 110°0'36"W, 45°21'36"N, 44°11'24"N). The exact extent was selected to include essentially all target species occurrence data to increase sample size for the model. The total study area was approximately 1.32 million hectares, representing 16.5% of the entire GYE land area (Yellowstone National Park 2016). The area has diverse habitat types: alpine tundra, conifer forests, sagebrush steppe, dry grasslands, wet meadows, sedge bogs, and willow bogs (Despain 1990). The elevation within the study area is between 1,550 m (5,090 ft) and 3,300 m (10,830 ft).

MODEL DEVELOPMENT

Species presence data were obtained from the Greater Yellowstone Coordinating Committee (GYCC), Northern Rocky Mountain Exotic Plant Management Team, YNP Exotic Plant Management Team, and the US Forest Service. Locations were represented by polygons surrounding infestations. Ground surveys were conducted July 10-13, 2018 and July 22-26, 2019 to refine polygons and digitize new polygons using Collector (Esri, Redlands, CA). Location data were converted from vectors to raster files at 20-m resolution in TerrSet (TerrSet v. 18.31, Clark Labs, Worcester, MA) then approximately 60% of the known occurrences (pixels) were used to develop the model (training data) and 40% were used to verify the model (validation data). Susceptibility models were created using the *Mahalanobis Typicality* approach in the *Habitat and Biodiversity Modeler: Habitat Suitability/Species Distribution Modeling* tool in TerrSet, incorporating ten environmental variables (i.e. aspect NS, aspect EW, slope, hill shade, precipitation, blue and green spectral bands, NDVI, NDWI, and [(NDWI +1) x (NDVI + 1)]) and training data for each species. (Words in *italics* indicate the name of tools or processing options within tools in TerrSet [Clark Labs, Worcester, MA] or ArcMap [Esri, Redlands, CA].) Meadow and orange hawkweed training data consisted of 60% of the total occurrence pixels so the remaining 40% could be used for model validation. The *Mahalanobis Typicality* modeling approach was most appropriate for presence only locations of meadow and orange hawkweed. *Mahalanobis Typicality* is a supervised classifier that assigns typicality probabilities to pixels based on their similarity to the training pixels. Values closer to 1 indicate high similarity to the mean of environmental conditions in training pixels.

Five spectral bands of Sentinel-2 data were downloaded for the study area from Earth Explorer USGS (European Space Agency 2018): blue (band 2, central λ=490 nm), green (band 3, central λ=560 nm), red (band 4, central λ=665), near-infrared (band 8a—NIR/vegetation red edge, central λ=865 nm) and short-wave infrared (band 10—SWIR, central λ=1610 nm. Red, green and blue bands were at 10-m resolution and NIR and SWIR bands were at 20-m resolution. Data were imported into TerrSet using *Government/Data Provider Formats* > *Sentinel* and selecting the reflectance correction: *Dark object subtraction* (*Top Of Atmosphere* correction gave the same values) (TerrSet v. 18.31, Clark Labs, Worcester, MA). Frames were *mosaiced* together then the study area was *windowed* (selected) from the larger area using tools in TerrSet. Red, green and blue bands were *contracted* from 10-m to 20-m resolution using pixel aggregation so they would have the same resolution as infrared bands. NDVI and NDWI were calculated using the 20-m resolution, Sentinel-2 data. NDVI and NDWI were combined to create a single variable to represent a moisture gradient of both. Each index was normalized by adding a value of one to remove negative values, then they were multiplied together [(NDWI +1) * (NDVI + 1)].

Average annual precipitation data were acquired from Parameter-elevation Regressions on Independent Slopes Model (PRISM 2015) for 2010 for an area with bounding coordinates 110° W, 114° W, 37° N, 49° N . The map was created from 30 arc-seconds (~800 m) PRISM grids at 10-m spatial resolution in decimal degrees for 2010. A 30-m resolution digital elevation model (DEM) was acquired from Earth Explorer USGS (2018). Precipitation and DEM maps were projected to UTM-12 and resampled to 20-m using the nearest neighbor technique in ArcMap (Esri, Redlands, CA). Precipitation ranged from 11 cm to 67 cm and was divided into 2 cm increments. Aspect, slope, and hill shade were derived from the DEM. Aspect was calculated in degrees then converted to radian.

$$\frac{(degrees \text{ x } \pi)}{180} = radian$$

Aspect represents the angle and amount of sunlight a surface receives. In the northern hemisphere, south facing slopes receive more direct sunlight than north facing slopes, and as previously mentioned, are typically drier. Aspect is a circular variable, for this reason it was split into a north-south and an east-west component so the model would recognize the

$$\text{R} = \text{aspect in radian}$$

$$\text{north-south} = \text{cosR}$$

$$\text{east-west} = \text{sinR}$$

similarity between 1° north and 359° north (Woodcock et al. 2008). For the north-south variable -1 is due south and 1 is due north. For the east-west variable a value of -1 is due west and a value of 1 is due east. Aspect was *exported* from ArcMap into *IMAGINE image files* then imported into TerrSet using *Software-Specific Formats* > *ERDAS.*

Seventeen different combinations of the environmental variables described above were tested in the *Habitat and Biodiversity Modeler: Habitat Suitability/Species Distribution Modeling* (TerrSet v. 18.31, Clark Labs, Worcester, MA) for predictions of meadow hawkweed susceptibility and orange hawkweed susceptibility (Table 1.1). Each model included north-south aspect, east-west aspect, and slope, along with one to five additional variables. Models were created at 20-m resolution but *contracted* (Contraction rule: *pixel aggregation*) to 40-m resolution and assessed based on a 9% error of commission rate for training data at 40-m resolution. The error rate was achieved by altering the range of *Mahalanobis Typicality* values for the "not susceptible" category of each model. The best model also minimized the percent of the study area predicted to be susceptible to meadow or orange hawkweed, thus reducing the area needed to be surveyed on foot, given the 9% error of commission for validation data.

Model effects on unsuitable habitat were compared to determine possible areas for improvement. Dense lodgepole pine (*Pinus contorta* Douglas ex Loudon) stands should be predicted not susceptible to meadow and orange hawkweed due to field observations of conditions. There were no documented meadow or orange hawkweed infestations within dense lodgepole pine stands in the study area, likely due to the lack of available resources on the forest floor. Sagebrush should be susceptible to meadow hawkweed but not susceptible to orange hawkweed based on locations of historic population and habitat preferences. Only populations of meadow hawkweed were documented in sagebrush communities within the study area.

REDUCING MODEL ERROR IN LODGEPOLE PINE STANDS

Lodgepole pine is an early successional tree species that forms dense stands, following fire disturbance, characterized by trees small in diameter, often short in comparison to neighboring stands, and sparse vegetation on the forest floor (Despain, 1990). No meadow or orange hawkweed populations were documented within dense stands, likely because of shading. However, the hawkweed susceptibility models predicted varying levels of susceptibility in areas of dense lodgepole pine, so a method was developed to identify and remove some of these lodgepole pine locations.

Fourteen polygons of dense lodgepole pines were digitized in the summer of 2019, ranging from 800 sq m to 15,800 sq m. Lodgepole pine polygons were overlaid on fire perimeters obtained from USDA fire records from 1889 to 2003 (Gibson 2005) in ArcMap (Esri, Redlands, CA). Fire data were used to identify the extent of potential dense lodgepole pine stands, based on time since fire. All digitized lodgepole pine polygons were within fires that occurred in 1988, meaning sites had 31 years to reach the current stage. Based on field observations, we assumed the inhospitable conditions for hawkweed establishment caused by the dense tree stands would be similar in stands 25 years and 37 years (31 years +/- 6) post fire. Therefore, fire polygons from 1982-1994 were extracted from the dataset. Next, fires polygons from 1995-2016 (USDA 1995-2002, Landfire 2003-2016) were *erased* from the dense lodgepole fire perimeters to ensure recently burned locations within the 25 to 37-year-old fire perimeters were not considered.

To predict locations of dense lodgepole pine, *Habitat and Biodiversity Modeler: Habitat Suitability/Species Distribution Modeling* (TerrSet v. 18.31, Clark Labs, Worcester, MA) was used across the entire study area, following methods described above for hawkweed models. Sixty percent of dense lodgepole pine pixels were used to train five models using different combinations of blue and green spectral bands, NDVI, NDWI, and precipitation (Table 1.2). As with the hawkweed models, the output was a map that assigned each pixel a value from 0 to 1 based on similarity to the training lodgepole pixels. The previously described fire region (25-37 years post fire) was then *windowed* (selected) from the full study area model. Model strength was determined by the proportion of dense lodgepole pine validation pixels properly classified in “predicted dense lodgepole pine”, and the proportion of open forest, meadow hawkweed and orange hawkweed classified as “not dense lodgepole pine.” The best dense lodgepole pine model was opened in ArcMap where mean *Focal Statistics* (Esri, Redlands, CA) were calculated with a 3-by-3-pixel rectangle. This resampling was used to ensure the edge habitat between dense lodgepole and open lodgepole stands were not removed from the hawkweed susceptibility models. Finally, the dense lodgepole pine model was imported back into TerrSet and *contracted* (Contraction rule: *pixel aggregation*) to 40-m pixels, then divided into “not dense lodgepole pine” and “predicted dense lodgepole pine” by *reclassifying* Mahalanobis Typicality values.

FINAL MODEL PROCESSING STEPS

A hydrologic features map was digitized in ArcGIS 10.6.1 (Esri, Redlands, CA) then imported into TerrSet (Clark Labs, Worcester, MA) as a vector and converted to a raster at 40-m resolution to remove water bodies. Removing roads was considered but since most paved roads in the study area were less than 15-m across, it did not seem appropriate to convert roads into 40-m pixels and lose susceptibility predictions adjacent to roads. Each susceptibility class was then converted to a vector and exported from TerrSet into ArcMap. Area for each susceptibility category was calculated in hectares.

PLANT COMMUNITY SURVEY DESIGN

Plant community surveys were conducted July 10-13, 2018 and July 22-26, 2019. Due to a late spring in 2019, seasonal variation in sampling times was minimal. Surveys were less than 1.2 km from a road in both years to increase the number of transects within the sampling window, though usually within 0.5 km. Each transect was 20-m long with five quadrats (i.e. plots), sized 0.25 m by 0.5 m, placed along the transect at 5-m intervals starting at 0-m. Within plots, the percent cover of bare ground, rock, and each plant species were estimated visually and assigned a ranked value based on estimated cover classes of: 0%, 1 to 5%, 5 to 12.5%, 12.5 to 25%, 25 to 50%, 50 to 75%, 75 to 95%, and 95 to 100%. Habitat types were identified using plant cover data from transects. Each transect was oriented to stay within a single community type. In 2018, all transects were within known locations of historic meadow hawkweed and orange hawkweed infestations. Known infestations were being managed by the Northern Rocky Mountain Invasive Plant Management Team so few if any hawkweed individuals were found along transects and the community was similar to pre-infestation conditions. In 2019 survey locations were selected based on a preliminary model's predictions. In 2019, survey locations were within several contiguous pixels of a susceptibility category from model predictions. Locations from 2018 were compared to model predictions and placed into the same susceptibility categories as 2019 data. A total of 43 transects were surveyed at elevations between 1,750 m (5,740 ft) and 2,430 m (7,970 ft).

INDICATOR SPECIES ANALYSIS

For analysis, cover data were converted to presence or absence only by transect. An indicator species analysis was conducted using a chi-squared test based on the occurrence of each hawkweed species against each species found on each transect (R v. 1.2.1335, Vienna, Austria). Orange and meadow hawkweed were considered to be present at a transect if they were seen in the area or if the transect was located within a treatment area of the Northern Rocky Mountain Exotic Plant Management Team. To obtain meaningful results, species found in fewer than three transects were removed from the statistical analysis but were considered for habitat typing. There were 66 species remaining for statistical testing. A Benjamini and Hochberg (1995) p-value adjustment was used to control the false discovery rate of significance. However, the adjusted p-values are provided only for context; they were not used for making selections of the significant species.

A quantitative measure of the indicator power (IP) of an indicator species for the target invasive species was calculated from a presence-absence matrix on species with chi-squared p-values < 0.05. A species is considered a strong indicator when it frequently co-occurs with the target invasive species while also infrequently occurring in the absence of the target. The IP equation:

$$\mathrm{IP}_I = \sqrt{\{[\mathrm{S} \div \mathrm{O}_I][1 - (\mathrm{O}_T - \mathrm{S}) \div (N - \mathrm{O}_I)]\}}$$

where O_I is the frequency of the indicator species (*I*) occurrence, O_T is the frequency of the target invasive species (*T*) occurrence, S is the frequency of shared occurrences of the indicator and the target species, and N is the total number of transects surveyed (Halme et al. 2009).

HABITAT TYPING

A vector layer for ArcMap and vegetation guide, both created by Despain (1990) who incorporated climax community and current conditions to determine habitat type, were used to identify habitat types at transect locations. Despain’s (1990) map is broad scale, transects were in habitat polygons 100 ha to 150,000 ha in size, so microhabitats were difficult to classify with this data alone. Due to disturbance, succession and scale, not all transects were classified as Despain (1990) had classified them. For refinement of habitat types Steele et al.

(1990) was used for forested habitats and Mattson (1984) was used for meadow and open riparian habitats. Transect photographs and species lists were compared to confirm habitat types.

RESULTS

SUSCEPTIBILITY MODELS

The best model prediction for meadow hawkweed was model 17: aspect NS, aspect EW, slope, NDVI, NDWI, band 2 (blue), band 3 (green), and precipitation (Table 1.1; Figure 1.4). Model 17 was selected because it predicted slightly less of the study area to be susceptible than other models and had the most agreement between training and validation data errors. The meadow hawkweed susceptibility was predicted to be 55.7% of the study area and error of commission for training and validation data was 8.9% and 6.4%, respectively (Table 1.3). Model 10 and 12 demonstrated the similarity between commission errors when using NDWI (model 10) or NDVI (model 12) with both aspect variables, slope and precipitation (Table 1.3). Model 3 and 10 accentuate the need for precipitation. Model 3 did not include precipitation and it predicted 72.5% of the study area to be susceptible verses 58.5% in model 10 which included precipitation. Precipitation also changed the distribution of susceptibility. Large areas that receive less than 15 cm or more than 50 cm precipitation annually were completely excluded from susceptibility.

The best model prediction for orange hawkweed was model 8: aspect NS, aspect EW, slope, NDVI, band 2, band 3, and precipitation (Table 1.1; Figure 1.5). Models 16 and 17 predicted less of the study area to be susceptible to orange hawkweed, 26.7% and 26.3%, respectively, compared to model 8. However, error of commission for validation pixels in models 16 and 17 were farther from the error of commission for their training data (Table 1.4). Model 12 also had a greater difference in error rates than model 8, and it predicted a larger area to be susceptible, 33.5%. Model 1 only used aspect variables, slope, and NDVI; it predicted 62.1% of the study area to be susceptible. Spectral bands and precipitation were necessary for the best orange hawkweed model prediction.

Models were divided into three susceptibility categories and a zero category to indicate no susceptibility based on the Mahalanobis Typicality values from the *Habitat and*

Biodiversity Modeler. The moderate and high categories for the final 40-m models were categorized at 0.4 to < 0.7 and 0.7 to 1.0. The minimum range of the low susceptibility category was set to ensure training data of meadow or orange hawkweed did not exceed a 9% error of commission rate. Meadow hawkweed categories were 0.0 to <0.083, 0.083 to < 0.40, 0.40 to < 0.70 and 0.70 to 1.0 (Table 1.8). Orange hawkweed categories were 0.0 to <0.173, 0.173 to <0.40, 0.40 to <0.70 and 0.70 to 1.0 (Table 1.9).

Approximately 414,800 ha (31.7%) of the study area was burned between 25 and 37 years ago and considered for dense lodgepole pine removal. The best model for dense lodgepole pine was model 4 which used NDVI, precipitation, band 2 and band 3 (Table 1.5). The area selected for removal (considered to be dense lodgepole pine) had a Mahalanobis Typicality value of $\geq$0.35. Dense lodgepole pine exclusion within the meadow hawkweed model was 7,518 ha (Table 1.6) and within the orange hawkweed model, 7,141 ha (Table 1.7). Incorporating dense lodgepole data into the models reduced the error of commission for dense lodgepole pine prediction within meadow and orange hawkweed susceptibility. Meadow hawkweed model went from 97.1% dense lodgepole error to 31.4% error (Table 1.6). Orange hawkweed model had an improvement from 94.3% error of dense lodgepole pine pixels to 28.6% error after the dense lodgepole pine model removal (Table 1.7).

The final results for the hawkweed models after dense lodgepole pine and hydrological feature removal indicated 55.1% of the study area was susceptible to meadow hawkweed (Table 1.8) and 29.1% of the study area was susceptible to orange hawkweed (Table 1.9). The portion of the study area in categories for meadow hawkweed susceptibility were: low, 38.2%, 499,534 ha ; moderate, 13.6%, 177,898 ha; and high, 3.4%, 44,217 ha (Table 1.8). Categories for orange hawkweed susceptibility were: low, 16.4%, 214,398 ha; moderate, 10.1%, 132,275 ha; and high, 2.6%, 33,645 ha of the study area (Table 1.9).

Overlaying susceptibility models indicated 551,669 ha (42.2%) of the study area was not susceptible to either hawkweed (Table 1.10). Overlapping areas of low susceptibility encompassed 118,587 ha (9.1%), overlapping moderate susceptibility encompassed 49,793 ha (3.8%), and overlapping high susceptibility encompassed 11,157 (0.9%)of the study area (Table 1.10). The area that was highly susceptible to meadow hawkweed but moderately susceptible to orange hawkweed was 16,964 ha (1.3%); the area moderately susceptible to meadow hawkweed and highly susceptible to orange hawkweed was 14,185 (1.1%). Area that was susceptible to meadow hawkweed but not susceptible to orange hawkweed was 376,654 ha (28.8%), of which, 314,579 ha (24.0%) were in the low category for meadow hawkweed susceptibility (Table 10). The area that was susceptible to orange hawkweed but not susceptible to meadow hawkweed was 35,325 ha (2.7%).Of which, 27,871 ha were in the low category for orange hawkweed susceptibility. Approximately 52.2% (376,654 ha) of meadow hawkweed susceptibility was not susceptible to orange hawkweed and 9.3% (35,325 ha) of orange hawkweed susceptibility is not susceptible to meadow hawkweed (Table 1.10).

SURVEYS: INDICATOR SPECIES

Forty-three transects were surveyed for plant cover in habitats predicted to be susceptible to meadow and orange hawkweeds based on model predictions. The meadow hawkweed model predicted 12 transects were in high susceptibility, 13 were in moderate susceptibility, 17 were in low susceptibility, and one was in the zero susceptibly category. In the orange hawkweed susceptibility model 13 transects were predicted to be in high, 11 predicted to be in moderate, 15 predicted to be in low, and five were in the zero-susceptibility category (Table 1.11). Of the 43 transects, 19 were in historic meadow or orange hawkweed infestations: seven in meadow hawkweed infestations, six in orange hawkweed infestations and six in infestations of both.

A total of 209 plant species were recorded within the 4 transects. Unknown species that occurred in fewer than 3 transects were not identified, leaving 143 identified species (Appendix A). *Carex* L. and *Equisetum* L. species were classified only to genus because plants were not in bloom. A few *Carex* individuals with flowers were identified to species but that information was only used for habitat typing, not statistical analyses. *Fragaria* L. species were also only recorded to genus. Only species that occurred in three or more transects were maintained for chi-square contingency test and indicator species analyses totaling 66 species. Chi-square contingency test revealed seven species were indicator species (p <0.05) for meadow hawkweed and three species were indicator species for orange hawkweed (Table 1.12). Adjusted p-values are reported for transparency but only the unadjusted p-values were used for selecting species for the indicator power analysis. *Carex* and *Equisetum* were comprised of multiple species but were included in the indicator species analysis because they were significantly associated with meadow hawkweed. Two of the species significantly associated with orange hawkweed were also significantly associated with meadow hawkweed, so overall the indicator power was assessed for eight species. Table 1.12 provides the chi-squared values, p-values, adjusted p-values, and indicator power (IP) for nine significant species (plus *Carex* and *Equisetum)* to show where differences in p-values and IP occur between those species for meadow and orange hawkweed.

The two significant species in common for both hawkweeds were Richard's geranium (*Geranium richardsonii* Fisch. & Trautv.) and fringed willowherb (*Epilobium ciliatum* Raf.) (Table 1.12). Species significantly associated only with meadow hawkweed were common selfheal (*Prunella vulgaris* L.), arrowleaf ragwort (*Senecio triangularis* Hook.), falsegold groundsel (*Packera pseudaurea* var. *pseudaurea* (Rydb.) W.A. Weber & Á. Löve), starry false lily of the valley (*Maianthemum stellatum* (L.) Link), and ballhead ragwort (*Senecio sphaerocephalus* Greene). The single species that was significantly associated only with orange hawkweed was alpine timothy (*Phleum alpinum* L.). All species significantly associated with meadow hawkweed had an IP of 0.998, showing strong indicator power (Table 1.12). The strongest indicators of orange hawkweed were fringed willowherb and Richard's geranium with IP values of 0.998 and 0.815, respectively. Alpine timothy had lower indicator power for orange hawkweed with an IP of 0.706, moderate indicator power. Species that were not significant in the chi-square analysis but were important in habitat typing included: bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) P. Beauv.), Idaho fescue *(Festuca idahoensis* Elmer), sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. Ex C.A. Mey.), yarrow (*Achillea millefolium* L.), lodgepole pine, basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*), Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), and *Vaccinium* spp. L.

SURVEYS: HABITAT TYPES

There were a total of 10 habitat types identified within predicted meadow and/or orange hawkweed susceptibility: big sagebrush (*Artemisia tridentata* Nutt.)/Idaho fescue, three transects; big sagebrush/Idaho fescue, sticky purple geranium phase, four transects; big sagebrush/bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve), two transects; Idaho fescue/bearded wheatgrass (*Elymus caninus* L.*)*, sticky purple geranium phase, six transect; lodgepole pine/Ross' sedge (*Carex rossii* Boott), 10 transects; subalpine fir (*Abies* *lasiocarpa* (Hook.) Nutt.)/grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville*)*, grouse whortleberry phase, seven transects; subalpine fir/bluejoint reedgrass, five transects; subalpine fir/western meadow-rue (*Thalictrum occidentale* A. Gray*)*, three transects; Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)/common snowberry (*Symphoricarpos albus* (L.) S.F. Blake), one transect; alpine timothy/water sedge (*Carex aquatilis* Wahlenb.), two transects (Table 1.13; Figure 1.7).

Predicted meadow hawkweed susceptibility encompassed all habitat types except Douglas-fir/common snowberry. However, only five habitat types were recorded within historic meadow hawkweed infestations (with or without orange hawkweed infestations): Idaho fescue/bearded wheatgrass, sticky purple geranium phase; lodgepole pine/Ross' sedge; subalpine fir/bluejoint reedgrass; alpine timothy/water sedge; and big sagebrush/Idaho fescue. The seven transects in historic infestations of only meadow hawkweed were in four habitat types: big sagebrush/bluebunch wheatgrass, one transect; Idaho fescue/bearded wheatgrass, sticky purple geranium phase, two transects; subalpine fir/bluejoint reedgrass, three transects; and subalpine fir/grouse whortleberry, grouse whortleberry phase, one transect (Table 1.13) (Despain 1990). The big sagebrush/bluebunch wheatgrass site was in a valley adjacent to the Gardiner River and was at the lowest elevation of all transects at 1,750 m. Although the meadow hawkweed model did not predict the area to be susceptibly it was retained and considered in "low susceptibility" because meadow hawkweed had been found at that location.

Predicted orange hawkweed susceptibility encompassed all habitat types except big sagebrush/Idaho fescue. Habitat types within historic orange hawkweed infestations (with or without meadow hawkweed infestations) were limited to four types: Idaho fescue/bearded wheatgrass, sticky purple geranium phase; lodgepole pine/Ross' sedge; subalpine fir/bluejoint reedgrass; and alpine timothy/water sedge. The six transects in historic infestation of only orange hawkweed were in just two habitat types: Idaho fescue/bearded wheatgrass, sticky purple geranium phase, four transects; and lodgepole pine/Ross' sedge, two transects. The four orange hawkweed transects in Idaho fescue/bearded wheatgrass (sticky purple geranium phase) were from two sites. One site was on a recent burn (< 20 years) with high forb diversity and the other site was a low area near the Lake Yellowstone marina with grasses and forbs. Each transect had 17-24 recorded species on the transect and no shading from trees. The two orange hawkweed transects in lodgepole pine/Ross' sedge were from one site within an opening in lodgepole pine canopy. Adjacent lodgepole pines were relatively young (~50 to 100 years post fire). Each transect categorized as lodgepole pine only had six species.

The six transects in combination meadow and orange hawkweed infestations were classified in three habitat types: subalpine fir/bluejoint reedgrass, two transects; lodgepole pine/Ross' sedge, two transects; or alpine timothy/water sedge, two transects (Despain 1990; Mattson 1984). The three transects classified as subalpine fir/bluejoint reedgrass did not have bluejoint reedgrass along the transects but all had arrowleaf ragwort on or adjacent to the transect and matched the site characteristics described in Mattson (1984). Although sedge species were not identified, transects were categorized in these habitat types based on other associated species and habitat descriptions (See Table 1.13 for descriptions).

DISCUSSION

In this study, we developed susceptibility models for meadow hawkweed and orange hawkweed using known locations and environmental data, determined indicator species and evaluated habitat types of both hawkweeds to assist land managers in their efforts to monitor and control these invasive plants in the GYE. Fifty-five percent of the study area is susceptible to invasion by meadow hawkweed and 29% is susceptible to orange hawkweed, after removing dense lodgepole pine from models. The similarities and differences in meadow and orange hawkweed susceptibility models suggest these species can co-occur across a wide range of habitats yet, a portion of their range is unique to each. Most of the differences in susceptible range to meadow and orange hawkweed occur at the margins of orange hawkweed suitable habitat. Orange hawkweed susceptibility primarily overlaps meadow hawkweed susceptibility, but meadow hawkweed susceptibility extends beyond the margins of the orange hawkweed range, intro drier plant communities.

When models overpredict susceptibility, it is beneficial to refine areas that are known to be unsuitable for infestation. Dense lodgepole pine stand are not suitable habitat for meadow or orange hawkweed so eliminating these areas from susceptibility reduced the model error. Sometimes it is difficult or impossible to refine model predictions in areas that have similar signatures to suitable habitat or particularly along the edge of two community types where one community is susceptible and the other is not. Removing dense lodgepole pine stands from the models was possible because the habitat had unique band 2, band 3, precipitation, and NDVI signatures. The edge of the dense lodgepole stands typically moved to a more open canopy that could be suitable for hawkweeds. The edge effect is why a much higher Mahalanobis Typicality value was selected for the dense lodgepole pine range (0.35-1.0) than for the hawkweed ranges (0.083-1.0 and 0.173-1.0), to ensure the potentially suitable edge habitat was not removed along with the dense lodgepole pine.

Although invasive hawkweeds are not typically found in dry shrub-steppe grasslands (Wilson 2006), a population of meadow hawkweed in the study area was within big sagebrush/Idaho fescue habitat type. The big sagebrush/Idaho fescue habitat type is a much drier community type than any orange hawkweed sites. Orange hawkweed may be found in sites with higher moisture than described in this study as it is known to infest bogs and cranberry fields (Jorgensen & Nauman, 1994). Wetter communities like willow and sedge dominated marshes were not surveyed here. There were 10 habitat types identified from plant community data acquired within predicted hawkweed susceptibility. Meadow hawkweed susceptibility encompassed all habitat types except Douglas-fir common snowberry. Orange hawkweed susceptibility encompassed all habitat types except big sagebrush/Idaho fescue. More GYE habitat types are at risk than have previously been documented by ground crews. While nine habitat types were identified within each model, historic hawkweed infestations were only in a total of five habitat types (meadow hawkweed found in all five, orange hawkweed only found in four). Using the susceptibility models to direct ground surveys in the novel habitat types that have not yet had documented invasions could be instrumental in locating new infestations and learning more about the invaders.

A challenge of developing susceptibility models for invasive species is the uncertainty if the invader is absent because the habitat is not suitable or simply because propagules have not yet made it into the area. This unknown is why presence only data were used to train the models. It is important to ensure the full range of environmental variables within location data are represented in the training data. The lowest elevation site for meadow hawkweed was included in model development but it was a small site, fewer than thirty 20-m pixels so it provided little influence on the model. Although elevation was not directly used in the model, associated environmental conditions may have been missed since this area was so small in comparison to the total training sites. Gaining location data can strengthen a model by increasing the sample size of training data. To build a reliable model it is important to have training data across the breadth of the invader's habitat. Models need to be recreated over time to incorporate changes in current environmental conditions (e.g. recent fires, floods, avalanches, long term droughts).

Using susceptibility models to predict areas susceptible to invasions has important implications for land managers, especially when ground survey-resources are limited (Shafii et al. 2003). Prioritizing areas highly likely to have suitable habitat for an invasive species can reduce the overall area that is surveyed, saving land managers time and money.

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Figure 1.1: Meadow hawkweed distribution

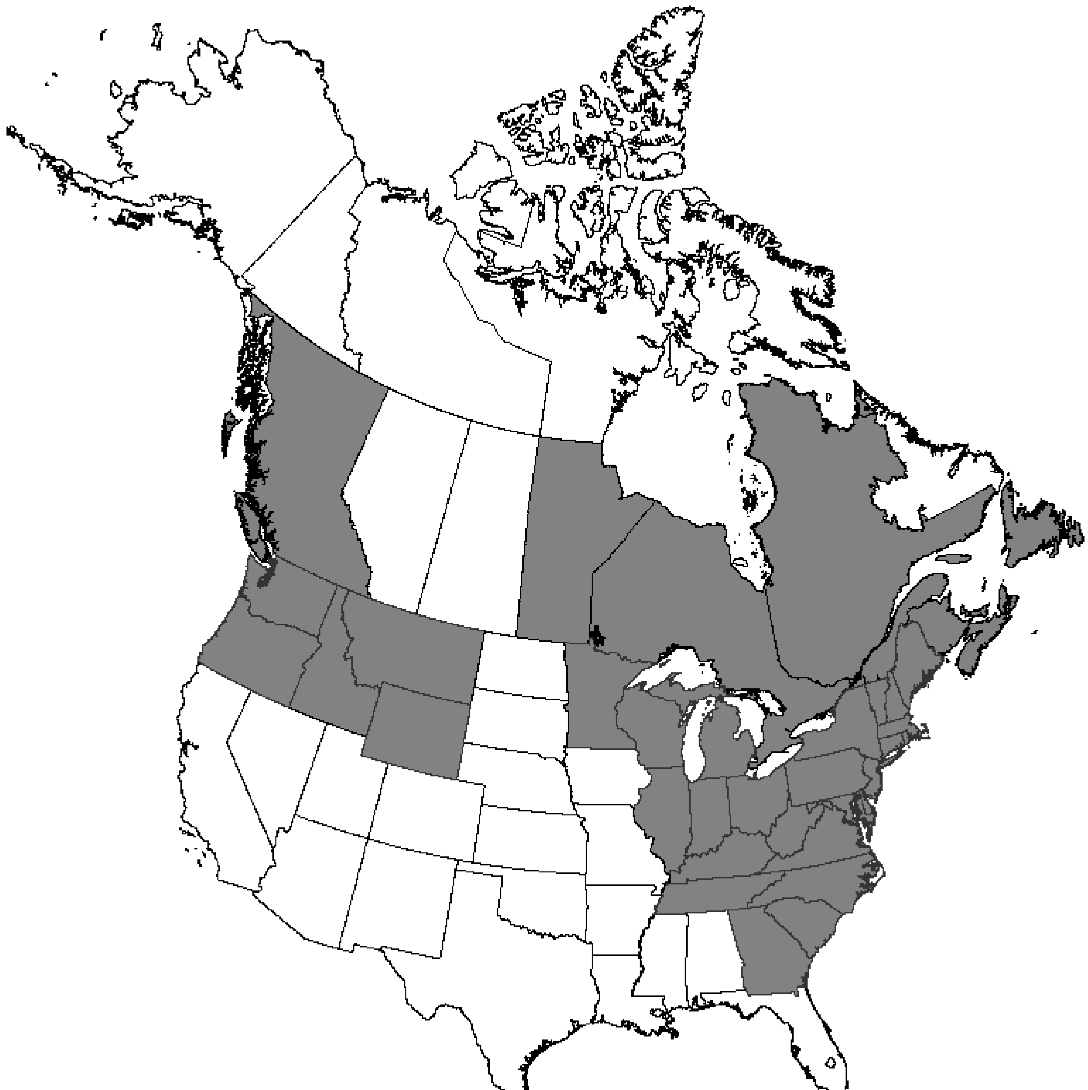


Figure 1.2: Orange hawkweed distribution

Figure 1.3: Study area within the Greater Yellowstone Ecosystem.

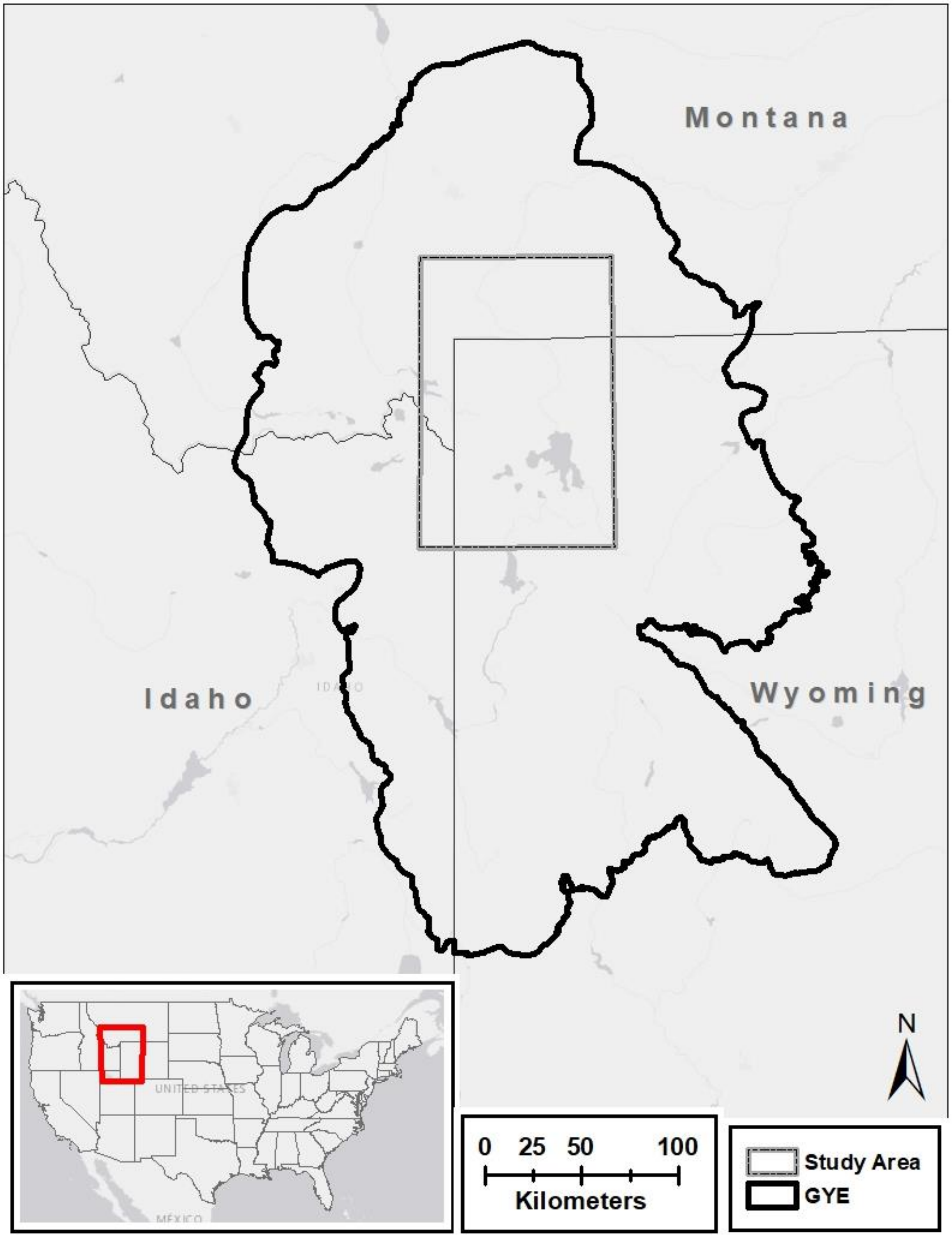


Table 1.1 Variables for model selection. Models include two aspect variables (north-south, east-west) (degrees) and slope (degrees) plus the indicated (x) variables above. Combinations tested to determine the best model for orange and meadow hawkweed. Sun angle diff. represents the difference in hillshading in August subtracted from hillshadding in May. Band 2 and band 3 are spectral bands, blue and green respectively.

	NDVI	sun angle diff.	NDWI	[(NDVI+1) *(NDWI+1)]	Band 2 (W sr^{-1} m^{-1})	Band 3 (W sr^{-1} m^{-1})	Precip. (cm)
Model 1	x						
Model 2	x	x					
Model 3			x				
Model 4	x		x				
Model 5				x			
Model 6	x				x		
Model 7	x				x		x
Model 8	x				x	x	x
Model 9			x		x		
Model 10			x				x
Model 11							x
Model 12	x						x
Model 13					x		x
Model 14	x		x		x		x
Model 15			x		x		x
Model 16			x		x	x	x
Model 17	x		x		x	x	x

Table 1.2 Dense lodgepole pine (DLP) model comparisons

	band 2	**band 3**	**NDWI**	**NDVI**	**precipitation**
DLP Model 1	x	x	x		
DLP Model 2	x	x		x	
DLP Model 3	x	x	x		x
DLP Model 4	x	x		x	x
DLP Model 5	x	x			x

Table 1.3 Meadow hawkweed model comparisons (40-m resolution). Each model has a zero category cut off that corresponds with 10% error for meadow hawkweed validation pixels. Zero category cut off from top to bottom:<0.083, <0.077, <0.078, <0.057, <0.117. .

		Training pixels	Validation pixels	Model Prediction (total study area)
Model 17				
	not susceptible	92	44	44.3%
	susceptible	941	639	55.7%
	total pixels	**1033**	**683**	
	error	8.9%	6.4%	
Model 16				
	not susceptible	92	37	41.8%
	susceptible	941	646	58.2%
	total pixels	**1033**	**683**	
	error	8.9%	5.4%	
Model 10				
	not susceptible	91	27	41.5%
	susceptible	942	656	58.5%
	total pixels	**1033**	**683**	
	error	8.8%	4.0%	
Model 12				
	not susceptible	92	28	33.4%
	susceptible	941	655	66.6%
	total pixels	**1033**	**683**	
	error	8.9%	4.1%	
Model 3				
	not susceptible	92	29	27.5%
	susceptible	941	654	72.5%
	total pixels	**1033**	**683**	
	error	8.9%	4.2%	

Table 1.4 Orange hawkweed model comparisons (40-m resolution). Each model has a zero category (not susceptible) cut off that corresponds with 9% error for orange hawkweed training pixels. Zero category cut off from top to bottom: <0.173, <0.197, <0.181, <0.137, <0.162.

		Training pixels	Validation pixels	Model Prediction (total study area)
Model 8				
	not susceptible	41	29	70.4%
	susceptible	427	271	29.6%
	total pixels	**468**	**300**	
	error	8.8%	9.7%	
Model 17				
	not susceptible	42	43	73.6%
	susceptible	426	257	26.4%
	total pixels	**468**	**300**	
	error	9.0%	14.3%	
Model 16				
	not susceptible	42	45	73.3%
	susceptible	426	255	26.7%
	total pixels	**468**	**300**	
	error	9.0%	15.0%	
Model 12				
	not susceptible	42	39	66.5%
	susceptible	426	261	33.5%
	total pixels	**468**	**300**	
	error	9.0%	13.0%	
Model 1				
	not susceptible	41	39	37.9%
	susceptible	427	261	62.1%
	total pixels	**468**	**300**	
	error	8.8%	13.0%	

Table 1.5 Dense Lodgepole Pine (DLP) Models . Number of meadow and orange hawkweed occurrence pixels (validation plus training pixels) within predicted DLP and not DLP for different DLP models at 20-m resolution. "Not DLP" corresponds to model Mahalanobis Value of <0.01.

		Meadow Hawkweed	**Orange Hawkweed**	**Open Forest**	**Dense Lodgepole Pine**	**Proportion of Study Area**
DLP Model 1	**not DLP**	4640	2428	119	9	NA
	DLP	984	429	32	82	4.57%
	Total	5624	2857	151	91	
	Error	**17.5%**	**15.0%**	**21.2%**	**9.9%**	
DLP Model 2	**not DLP**	4741	2495	125	8	NA
	DLP	883	362	26	83	4.58%
	Total	5624	2857	151	91	
	Error	**15.7%**	**12.7%**	**17.2%**	**8.8%**	
DLP Model 3	**not DLP**	4688	2550	134	10	NA
	DLP	936	307	17	81	1.82%
	Total	5624	2857	151	91	
	Error	**16.6%**	**10.7%**	**11.3%**	**11.0%**	
DLP Model 4	**not DLP**	4736	2585	135	9	NA
	DLP	888	272	16	82	1.94%
	Total	5624	2857	151	91	
	Error	**15.8%**	**9.5%**	**10.6%**	**9.9%**	
DLP Model 5	**not DLP**	4633	2498	140	9	NA
	DLP	991	359	11	82	2.57%
	Total	5624	2857	151	91	
	Error	**17.6%**	**12.6%**	**7.3%**	**9.9%**	

Table 1.6 Error rate for dense lodgepole pine (DLP) pixels in final meadow hawkweed model (model 17). Before and after DLP removal at 40-m resolution with the zero category <0.083. Sagebrush pixels reported for model before and after DLP removal, though no error rate is calculated because portions of sagebrush habitat are susceptible to meadow hawkweed. Removing DLP—Model 4 (all values 0.35 and above) improved DLP error rate from 97.1% to 31.4%, thus reducing the over estimation of predicted susceptibility to meadow hawkweed. Meadow hawkweed susceptibility was reduced by 7,518 ha.

		ALL OCCURRENCE PIXELS		
		Dense Lodgepole Pine	**Sagebrush**	**Study Area**
Before DLP removal	**not susceptible**	1	29	579,445 ha
	susceptible	34	30	729,167 ha
	total pixels	35	59	
	error	**97.1%**	**NA**	
		Dense Lodgepole Pine	**Sagebrush**	**Study Area**
After DLP removal	**not susceptible**	24	29	586,993 ha
	susceptible	11	30	721,649 ha
	total pixels	35	59	
	error	**31.4%**	**NA**	

Table 1.7 Error rate for dense lodgepole pine (DLP) pixels and sagebrush pixels in final orange hawkweed model (model 8) before and after (DLP) removal at 40-m resolution with the zero category <0.173. Removing DLP—Model 4 (all values 0.35 and above) improved DLP error rate from 94.3% to 28.6%, thus reducing the over estimation of predicted susceptibility to orange hawkweed. Orange hawkweed susceptibility was reduced by 7,141 ha. Sagebrush pixels reported for comparison; no change to sagebrush error rate.

		ALL OCCURRENCE PIXELS		
		Dense Lodgepole Pine	**Sagebrush**	**Study Area**
Before DLP removal	**not susceptible**	2	29	**921,182 ha**
	susceptible	33	30	**387,460 ha**
	total pixels	35	59	
	error	**94.3%**	**50.1%**	
		Dense Lodgepole Pine	**Sagebrush**	**Study Area**
After DLP removal	**not susceptible**	25	29	**928,323 ha**
	susceptible	10	30	**380,319 ha**
	total pixels	35	59	
	error	**28.6%**	**50.1%**	

Table 1.8 Meadow hawkweed susceptibility categories at 40-m resolution, after DLP removal.

Susceptibility Categories	**Mahalanobis Typicality Values**	**Percent of Study Area**	**Total Hectares**	**Training Pixels**	**Validation Pixels**
not susceptible	0.000 < x < 0.083	44.9	586,993	95	88
low	0.083 < x < 0.40	38.2	499,534	275	163
moderate	0.40 < x < 0.70	13.6	177,898	274	161
high	0.70 < x ≤ 1.0	3.4	44,217	389	271
total pixels				1033	683

Figure 1.4: Meadow hawkweed susceptibility model (after DLP removal).

Table 1.9 Orange hawkweed susceptibility categories at 40-m resolution, after DLP removal.

Susceptibility Categories	Mahalanobis Typicality Values	Percent of Study Area	Total Hectares	Training Pixels	Validation Pixels
not susceptible	0.000 < x < 0.173	70.9	928,323	42	57
low	0.173 < x < 0.40	16.4	214,398	77	76
moderate	0.40 < x < 0.70	10.1	132,275	154	96
high	0.70 < x ≤ 1.0	2.60	33,645	195	71
total pixels				468	300

Figure 1.5: Orange hawkweed susceptibility model (after DLP removal).

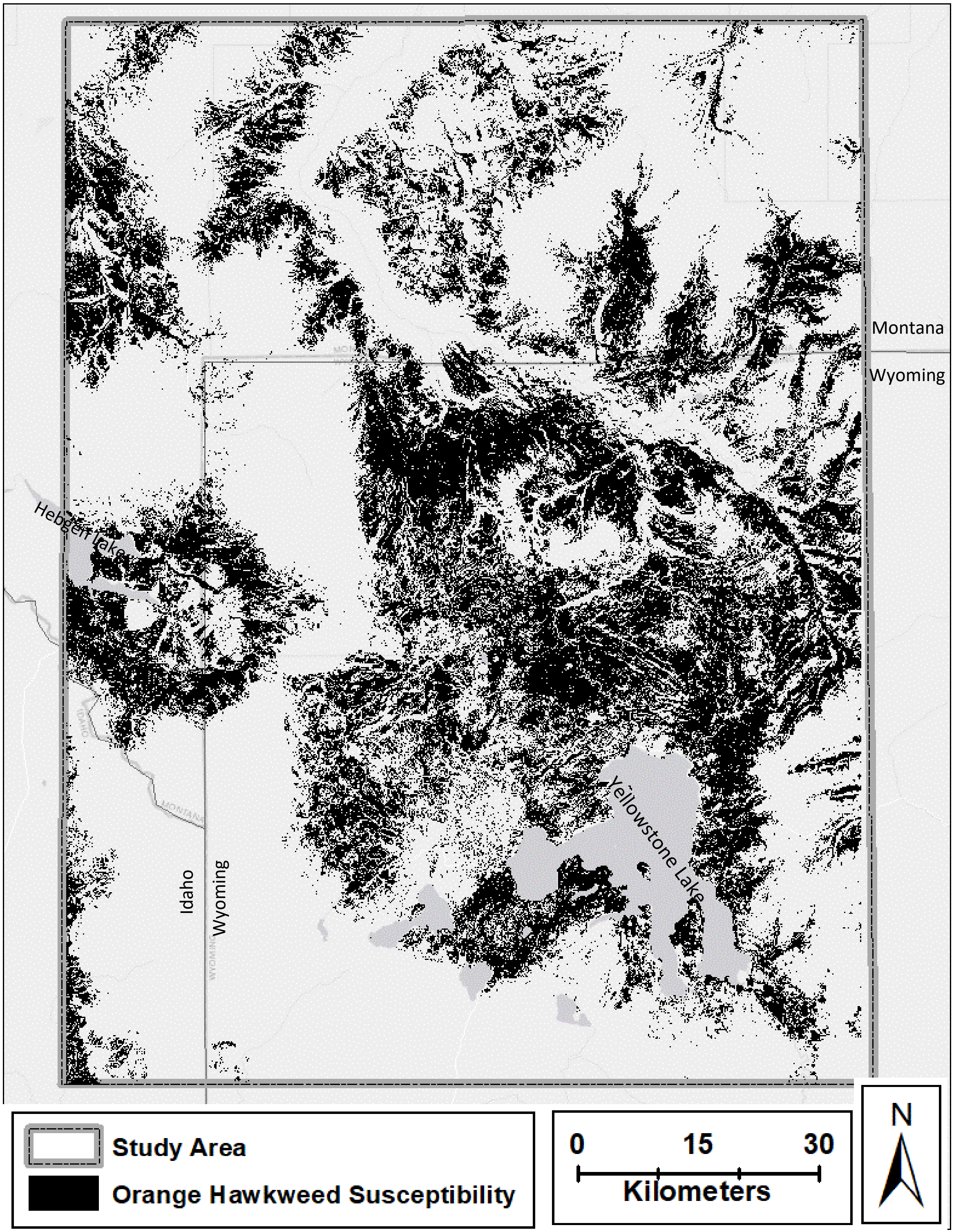


Table 1.10 Meadow and orange hawkweed susceptibility model overlap. Hectares and percent of study area in meadow and orange hawkweed susceptibility overlap (after DLP removal). The first value, 551,669 ha and 42.2% indicates the portion of the study area not susceptible to either hawkweed.

	ha	percentage	ha	percentage	ha	percentage	ha	percentage
meadow hawkweed categories (across)	zero		low		moderate		high	
orange hawkweed categories (down)								
zero	551,669	42.2	314,579	24.0	58,518	4.5	3,557	0.3
low	27,871	2.2	118,587	9.1	55,404	4.2	12,538	1.0
moderate	7,010	0.5	58,509	4.5	49,793	3.8	16,964	1.3
high	444	0.0	7,860	0.6	14,185	1.1	11,157	0.9

Table 1.11: Number of transects in each susceptibility category for meadow and orange hawkweed.

		Meadow Hawkweed				Orange Hawkweed
		high	mod	low	zero	sum
Orange Hawkweed	high	9	3	1	0	13
	mod	3	5	3	0	11
	low	0	5	9	1	15
	zero	0	0	5	0	5
Meadow Hawkweed	sum	12	13	18	1	

Figure 1.6: Orange hawkweed susceptibility model over meadow hawkweed susceptibility model (after DLP removal). The majority of the area susceptible to orange hawkweed (red) is also susceptible to meadow hawkweed (black). Meadow hawkweed susceptibility extends beyond orange hawkweed susceptibility.

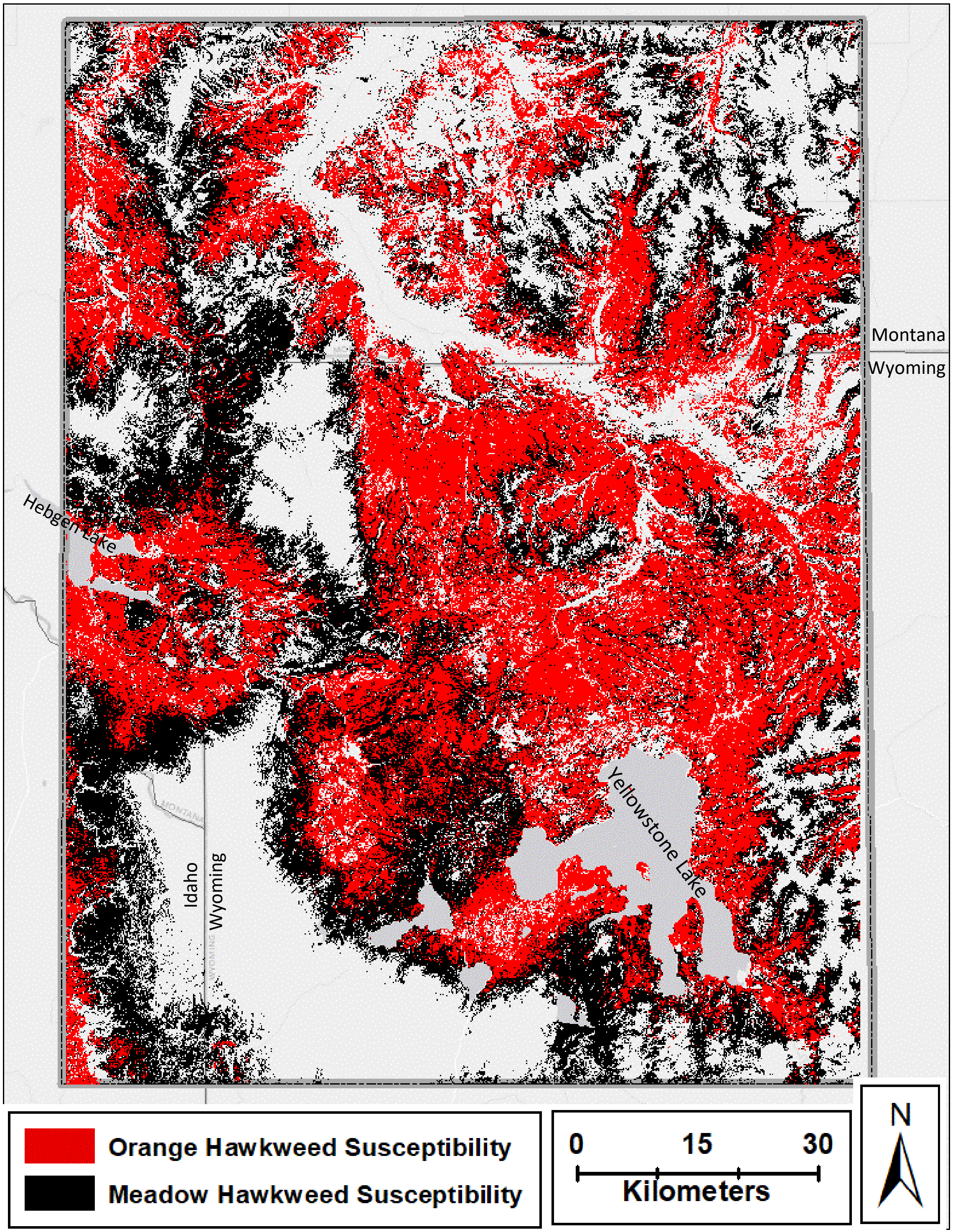


Table 1.12 Indicator species results

	Meadow Hawkweed				Orange Hawkweed			
Species	**chi-sq**	**p-value**	**adj p-value**	**IP**	**chi-sq**	**p-value**	**adj p-value**	**IP**
Richard's geranium	16.09	<0.001*	0.064	0.998	5.21	0.039*	0.531	0.815
Equisetum spp	13.06	0.002*	0.075	0.889	2.90	0.116	0.544	0.678
arrowleaf ragwort	10.18	0.003*	0.075	0.998	1.07	0.561	0.898	0.705
common selfheal	10.18	0.008*	0.128	0.998	4.86	0.060	0.531	0.864
falsegold groundsel	7.44	0.016*	0.211	0.998	2.41	0.185	0.544	0.814
starry false lily of the valley	7.44	0.021*	0.224	0.998	0.05	1.000	1.000	0.576
ballhead ragwort	7.44	0.027*	0.240	0.998	2.41	0.173	0.544	0.814
fringed willowherb	7.44	0.030*	0.240	0.998	8.33	0.015*	0.531	0.998
Carex spp.	5.37	0.045*	0.323	0.625	1.94	0.195	0.544	0.548
alpine timothy	3.85	0.073	0.426	0.706	5.04	0.032*	0.531	0.706

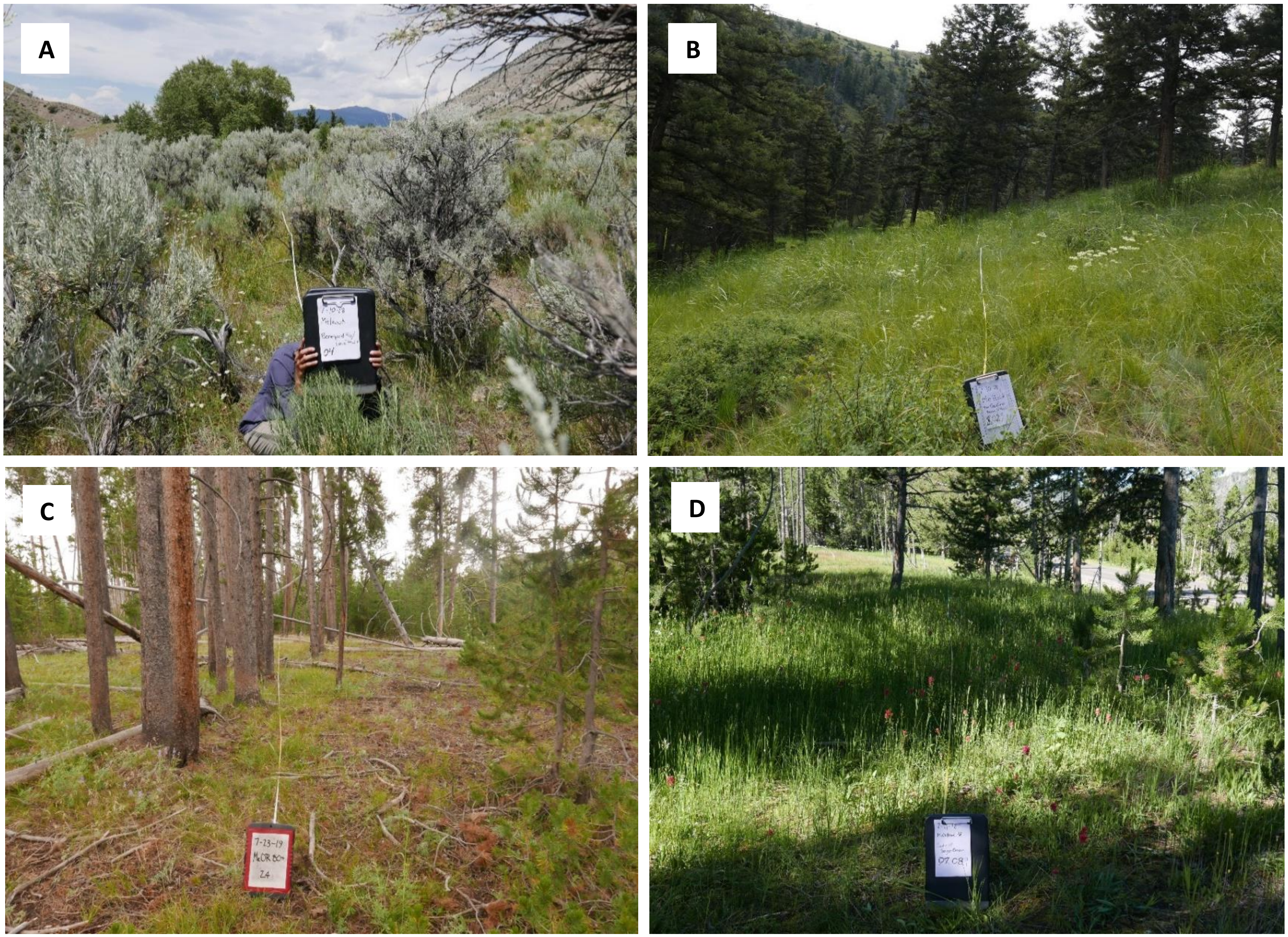
* indicates significant p-value

Table 1.13 Habitat type descriptions at transects. Habitat type descriptions from Despain (1990). Additional descriptions were included form Steele et al. (1990) and Mattson (1984). The altitude range from Despain (1990) is included however, his GIS layer had some discrepancies. For example, the book listed big sagebrush/Idaho fescue occurring at 6,800-9,500 ft but a portion of the map labeled as big sagebrush/Idaho fescue was at 5,400 ft.

Vegetation Type	Habitat Type	Altitude (meters)	Habitat description	Elevation of transects (m)	Number of Transects
Shrubland/ grassland	Big Sagebrush/ FIED	2,100 -2,900	Moist shrubland of big sagebrush and Idaho fescue, occasionally with bluebunch wheatgrass. Prairie smoke, fringed sagebrush, rabbit brush and junegrass are common.	1,750 - 1,880	3
	Big Sagebrush/ FIED Phase: sticky purple geranium	2,100 - 2,900	This phase is more moist, denser ground cover of grasses and forbs; sticky purple geranium, California brome, sulfur buckwheat, graceful cinquefoil bearded wheatgrass, Raynold's sedge	1,910 - 2,370	4
	Big Sagebrush/PSSP	1,800+	Dry shrubland with big sagebrush interspersed with bluebunch wheatgrass. Other common plants include junegrass, Sandberg's bluegrass, needle-and-thread	1,980 - 2,010	2
Grassland/ meadow	Idaho fescue/bearded wheatgrass Phase: sticky purple geranium	2,300 - 3,000	High moisture; pocket-gopher activity, FEID nearly absent taller forbs common sticky purple geranium and graceful cinque foil are indicators. Other common species include yampah, goldenrod, California brome and giant frasera	1,990 - 2,430	6
	Alpine timothy/*Carex aquatilis*	(from Mattson 1984, no elevation given)	Alpine timothy, *Carex aquatilis, Antenaria corymbose, Calamagrostis canadensis, carex microptera, Senecio sphaerocephalus, Geum macrophylum, Fragaria viriniana, Viola adunca, Potentilla diversifolia.* Moderate number of species (19-27 sp/50 m^2), moist meadow.	2,270	2

Wet Forest	Lodgepole pine/Ross' sedge	2,100 -2,400	Lodgepole pine, silvery lupine, northern goldenrod, Ross' sedge, Wheeler's bluegrass. (Although Despain 1990 says it is typically on steep, south-facing slopes, Steele et al. 1983 notes within Yellowstone NP this habitat type is on gentile terrain at mid-elevations)	2,080 - 2,500	9
Open Forests	Subalpine Fir/Grouse Whortleberry Phase: grouse whortleberry	2,000 -2,400	Lodgepole pine, Englemann spruce, subalpine fir, Douglas-fir, whortleberry, heart leaf arnica, elk sedge, mosses and lichens	2,080 - 2,490	7
	Subalpine fir/bluejoint	2,000 -2,100	Lodgepole pine, Englemann spruce, subalpine fir, bluejoint reedgrass. Typically along stream or ponds. These transects were identified in this habitat type based on characteristics in Mattson (1984) of bluejoint reedgrass/ bluejoint reedgrass habitat type which are typically surrounded by shading forest, high species diversity (23-42 sp/50m^2). Additional species present include arrowleaf ragwort, yarrow, *Fragaria sp.*	2,220 - 2,380	5
	Subalpine fir/western meadow-rue	2,300 – 2,700	Lodgepole pine, subalpine fir, mountain sweetroot, pinegrass, heartleaf arnica, fireweed, western meadow-rue, mountain gooseberry	2,000 – 2,480	3
	Douglas-fir/common snowberry	1,800 - 2,300	Douglas-fir, common snowberry, lodgepole pine, aspen, service berry, western yarrow, pinegrass	1,800	1

Figure 1.7— Meadow and orange hawkweed habitat types. A) basin big sagebrush/Idaho fescue, only susceptible to meadow hawkweed. B) Douglas-fir/common snowberry, only susceptible to orange hawkweed. C) Lodgepole pine/sedges, susceptible to meadow and orange hawkweed. D) subalpine fir/bluejoint grass susceptible to meadow and orange hawkweed.



Appendix A **Transect species**

Common Name	**Species**	**Authority**	**Family**	**Code**
common cowparsnip	*Heracleum maximum*	W. Bartram	Apiaceae	HEMA80
Gairdner's yampah	*Perideridia gairdneri*	(Hook. & Arn.) Mathias	Apiaceae	PEGA3
star flowered false solomon's seal	*Maianthemum stellatum*	(L.) Link	Asparagaceae	MAST4
common yarrow	*Achillea millefolium*	L.	Asteraceae	ACMI2
orange agoseris	*Agoseris aurantiaca*	(Hook.) Greene	Asteraceae	AGAU2
Lyall's angelica	*Angelica arguta*	Nutt.	Asteraceae	ANAR3
low pussytoes	*Antennaria dimorpha*	(Nutt.) Torr. & A. Gray	Asteraceae	ANDI2
western pearly everlasting	*Anaphalis margaritacea*	(L.) Benth.	Asteraceae	ANMA
littleleaf pussytoes	*Antennaria microphylla*	Rydb.	Asteraceae	ANMI3
small-leaf pussytoes	*Antennaria parvifolia*	Nutt.	Asteraceae	ANPA4
rosy pussytoes	*Antennaria rosea*	Greene	Asteraceae	ANRO2
heartleaf arnica	*Arnica cordifolia*	Hook.	Asteraceae	ARCO9
prairie sagewort	*Artemisia frigida*	Willd.	Asteraceae	ARFR4
hairy arnica	*Arnica mollis*	Hook.	Asteraceae	ARMO4
Rydberg's arnica	*Arnica rydbergii*	Greene	Asteraceae	ARRY
basin big sagebrush	*Artemesia tridentata ssp. tridentata*	Nutt.	Asteraceae	ARTRT
mountain big sagebrush	*Artemesia tridentata* Nutt. *ssp. vaseyana*	(Rydb.) Beetle	Asteraceae	ARTRV
Wyoming big sagebrush	*Artemesia tridentata* Nutt. *ssp. wyomingensis*	Beetle & Young	Asteraceae	ARTRW8
arrowleaf balsomroot	*Balsamorhiza sagittata*	(Pursh) Nutt.	Asteraceae	BASA3
yellow rabitbrush	*Chrysothamnus viscidiflorus*	(Hook.) Nutt.	Asteraceae	CHVI8
Canada thistle	*Cirsium arvense*	(L.) Scop.	Asteraceae	CIAR4
elk thistle	*Cirsium foliosum*	(Hook.) DC.	Asteraceae	CIFO
meadow/Everats' Thistle	*Cirsium scariosum*	Nutt.	Asteraceae	CISC2
bull thistle	*Cirsium vulgare*	(Savi) Ten.	Asteraceae	CIVU
tapertip hawksbeard	*Crepis acuminata*	Nutt.	Asteraceae	CRAC2
threadleaf fleabane	*Erigeron filifolius*	(Hook.) Nutt.	Asteraceae	ERFI2

rubber rabbitbrush	*Ericameria nauseosa*	(Pall. ex Pursh) G.L. Nesom & Baird	Asteraceae	ERNA10
aspen fleabane	*Erigeron speciosus*	(Lindl.) DC.	Asteraceae	ERSP4
Engelmann's aster	*Eucephalus engelmannii*	(D.C. Eaton) Greene	Asteraceae	EUEN
white hawkweed	*Hieracium albiflorum*	Hook.	Asteraceae	HAL2
orange hawkweed	*Hieracium aurantiacum*	L.	Asteraceae	HIAU
oneflower helianthella	*Helianthella uniflora*	(Nutt.) Torr. & A. Gray	Asteraceae	HEUN
meadow hawkweed	*Hieracium caespitosum*	Dumort.	Asteraceae	HICA10
yellow hawkweed	*Hieracium fendleri*	Sch. Bip.	Asteraceae	HIFE
hairy albert	*Hieracium scouleri Hook. var. albertinum*	(Farr) G.W. Douglas & G.A. Allen	Asteraceae	HISCA
hoary tansyaster	*Machaeranthera canescens*	(Pursh) A. Gray	Asteraceae	MACA2
falsegold groundsel	*Packera pseudaurea var. pseudaurea*	(Rydb.) W.A Weber & A. Löve	Asteraceae	PAPSP2
ballhead ragwort	*Senecio sphaerocephalus*	Greene	Asteraceae	SESP4
arrowleaf ragwort	*Senecio triangularis*	Hook.	Asteraceae	SETR
rocky mountain goldenrod	*Solidago multiradiata*	Aiton	Asteraceae	SOMU
longleaf/western aster	*Symphyotrichum ascendens*	(Lindl.) G.L. Nesom	Asteraceae	SYAS3
common dandelion	*Taraxacum officinale*	F.H. Wigg.	Asteraceae	TAOF
spineless horsebrush	*Tetradymia canescens*	DC.	Asteraceae	TECA2
yellow salsify	*Tragopogon dubius*	Scop.	Asteraceae	TRDU
Oregon grape	*Manonia aquafolia*	(Pursh) Nutt.	Berberidaceae	MAAQ2
houndstongue/gypsyflower	*Cynoglossum officinale*	L.	Boraginaceae	cyof
manyflower stickseed	*Hackelia floribunda*	(Lehm.) I.M. Johnst.	Boraginaceae	HAFL2
western stoneseed	*Lithospermum ruderale*	Douglas ex Lehm.	Boraginaceae	LIRU4
Asian forget-me-not	*Myosotis asiatica*	(Vesterg.) Schischkin & Sergievskaja	Boraginaceae	MYAS2
Cusick's rockcress	*Arabis cusickii*	S. Watson	Brassicaceae	ARCU
western tansymustard	*Descurainia pinnata*	(Walter) Britton	Brassicaceae	DEPI
tall tumblemustard	*Sisymbrium altissimum*	L.	Brassicaceae	SIAL2
field pennycress	*Thlaspi arvense*	L.	Brassicaceae	THAR5

desert madwort	*Alyssum desertorum*	Stapf.	Brassicaea	ALDE
bluebell bellflower	*Campanula rotundifolia*	L.	Campanulaceae	CARO2
common snowberry	*Symphoricarpos albus*	(L.) S.F. Blake	Caprifoliaceae	SYAL
ballhead sandwort	*Arenaria congesta*	Nutt.	Caryophyllaceae	ARCO5
Field Chickweed	*Cerastium arvense*	L.	Caryophyllaceae	CEAR4
common/mouse-ear chickweed	*Cerastium fontanum*	L.	Caryophyllaceae	CEFO2
bladder campion	*Silene latifolia*	Poir.	Caryophyllaceae	SILA21
corn spurry	*Spergula arvensis*	L.	Caryophyllaceae	SPAR
field bindweed	*Convolvulus arvensis*	L.	Convolvulaceae	COAR4
Rocky Mountain juniper	*Juniperus scopulorum*	Sarg.	Cupressaceae	JUSC2
Douglas' sedge	*Carex douglasii*	Boott	Cyperaceae	CAREX
Northwest Territory sedge	*Carex utriculata*	Boott	Cyperaceae	CAREX
horsetail	*Equisetum sp*	L.	Equisetaceae	EQUIS
velvetleaf huckleberry	*Vaccinium myrtilloides*	Michx.	Ericaceae	VAMY
whortleberry	*Vaccinium myrtillus*	L.	Ericaceae	VAMY2
prairie milkvetch	*Astragalus adsurgens*	(Hook.) Barneby & S.L. Welsh	Fabaceae	ASLAR
milkvetch	*Astragalus*	L.	Fabaceae	ASTRA
Lupine	*Lupinus sp.*	L.	Fabaceae	LUPIN
black medick	*Medicago lupulina*	L.	Fabaceae	MELU
sweetclover	*Melilotus officinalis*	(L.) Lam.	Fabaceae	MEOF
red clover	*Trifolium pratense*	L.	Fabaceae	TRPR2
white clover	*Trifolium repens*	L.	Fabaceae	TRRE3
vetch	*Vicia*	L.	Fabaceae	VICIA
Richardson's geranium	*Geranium richardsonii*	Fisch. & Trautv.	Geraniaceae	GERI
sticky purple geranium	*Geranum viscosissimum*	Fisch. & C.A. Mey. ex C.A. Mey.	Geraniaceae	GEVI2
common selfheal	*Prunella vulgaris*	L.	Lamiaceae	PRVU
Lewis flax	*Linum lewisii*	Pursh	Linaceae	LILE3
narrowleaf fireweed	*Chamerion augustifolium*	(L.) Holub	Onagraceae	CHAN9

tall annual willowherb	*Epilobium brachycarpum*	C. Presl	Onagraceae	EPBR3
fringed willowherb	*Epilobium ciliatum*	Raf.	Onagraceae	EPCI
leafy willowherb	*Epilobium foliosum*	(Torr. & A. Gray) Suksd.	Onagraceae	EPFO*?
milkflower willowherb	*Epilobium lactiflorum*	Hausskn.	Onagraceae	EPLA3
zigzag groundsmoke	*Gayophytum heterozygum*	F.H. Lewis & Szweykowski	Onagraceae	GAHE3
white bog orchid, scentbottle	*Platanthera dilatate*	(Pursh) Lindl. ex Beck	Orchidaceae	PLDI3
Wyoming Indian paintbrush	*Castilleja linariifolia*	Benth.	Orobanchaceae	CALI4
lodgepole pine	*Pinus contorta*	Douglas ex Loudon	Pinaceae	PICO
Douglas-fir	*Pseudotsuga menziesii*	(Mirb.) Franco	Pinaceae	PSME
narrowleaf plantain	*Plantago lanceolata*	L.	Plantaginaceae	PLLA
Columbia needlegrass	*Achnatherum nelsonii*	(Scribn.) Barkworth	Poaceae	ACNE9
rough bentgrass	*Agrostis scabra*	Willd.	Poaceae	AGSC5
purple threeawn	*Aristida purpurea*	Nutt.	Poaceae	ARPU9
field brome	*Bromus arvensis*	L.	Poaceae	BRAR5
mountain brome	*Bromus marginatus*	Nees ex Steud.	Poaceae	BRMA4
cheatgrass	*Bromus tectorum*	L.	Poaceae	BRTE
bluejoint reedgrass	*Calamagrostis canadensis*	(Michx.) P. Beauv.	Poaceae	CACA4
onespike danthonia	*Danthonia unispicata*	(Thurb.) Munro ex Macoun	Poaceae	DAUN
Canada wildrye	*Elymus canadensis*	L.	Poaceae	ELCA4
squirreltail	*Elymus elymoides*	(Raf.) Swezey	Poaceae	ELEL5
thickspike wheatgrass	*Elymus lanceolatus*	(Scribn. & J.G. Sm.) Gould	Poaceae	ELLA3
slender wheatgrass	*Elymus trachycaulus* ssp. trachycaulus	(Link) Gould ex Shinners	Poaceae	ELTRT
Idaho Fescue	*Fescue idahoensis*	Elmer	Poaceae	FEID
mannagrass	*Glyceria grandis*	S. Watson	Poaceae	GLGR
basin wildrye	*Leymus cinereus*	(Scribn. & Merr.) Á. Löve	Poaceae	LECI4
green needlegrass	*Nassella viridula*	(Trin.) Barkworth	Poaceae	NAVI4
western wheatgrass	*Pascopyrum smithii*	(Rydb.) Á. Löve	Poaceae	PASM
alpine timothy	*Phleum aplinum*	L.	Poaceae	PHAL2
timothy	*Phleum pratense*	L.	Poaceae	PHPR3

alpine bluegrass	*Poa alpina*	L.	Poaceae	POAL2
Canada bluegrass	*Poa compressa*	L.	Poaceae	POCO
muttongrass	*Poa fendleriana*	(Steud.) Vasey	Poaceae	POFE
Kentucky bluegrass	*Poa pratensis*	L.	Poaceae	POPR
sandberg bluegrass	*Poa secunda*	J. Presl	Poaceae	POSE
bluebunch wheatgrass	*Pseudoroegneria spicata*	(Pursh) Á. Löve	Poaceae	PSSP6
spike trisetum	*Trisetum spicatum*	(L.) K. Richt	Poaceae	TRSP
tiny trumpet	*Collomia linearis*	Nutt.	Polemoniaceae	COLI2
spiny phlox	*Phlox hoodii*	Richardson	Polemoniaceae	PHHO
longleaf phlox	*Phlox longifolia*	Nutt.	Polemoniaceae	PHLO2
parsnipflower buckwheat	*Eriogonum heracloides*	Nutt.	Polygonaceae	ERHE2
sulfur-flower buckwheat	*Eriogonum umbellatum*	Torr.	Polygonaceae	ERUM
Americaon bistort	*Polygonum bistortoides*	Pursh	Polygonaceae	POBI6
large knotweed	*Polygonum douglasii Green ssp. majus*	(Meisn.) J.C. Hickman	Polygonaceae	PODOM2
common sheep sorrel	*Rumex acetosella*	L.	Polygonaceae	RUAC3
Columbian monkshood	*Aconitum columbianum*	Nutt.	Ranunculaceae	ACCO4
woodland buttercup	*Ranunculus uncinatus*	D. Don ex G. Don	Ranunculaceae	RAUN
western meadow-rue	*Thalictrum occidentale*	A. Gray	Ranunculaceae	THOC
snowbrush ceanothus	*Ceanothus velutinus*	Doublas ex Hook.	Rhamnaceae	CEVE
shrubby cinquefoil	*Dasiphora fruticosa*	(L.) Rydb.	Rosaceae	DAFR6
wild strawberry	*Fragaria sp.*	L.	Rosaceae	FRAGA
prairie smoke	*Geum triflorum*	Pursh	Rosaceae	GETR
siör cinquefoil	*Potentilla argentea*	L.	Rosaceae	POAR8
slender cinquefoil	*Potentilla gracilis*	Douglas ex Hook.	Rosaceae	POGR9
sulfur cinquefoil	*Potentilla recta*	L.	Rosaceae	PORES
chokecherry	*Prunus virginiana*	L.	Rosaceae	PRVI
Woods' rose	*Rosa woodsii*	Lindl.	Rosaceae	ROWO
white/birchleaf spirea	*Spiraea betulifolia*	Pall.	Rosaceae	SPBE2
northern bedstraw	*Galium boreale*	L.	Rubiaceae	GABO2
bastard toadflax	*Comandra umbellata*	(L.) Nutt.	Santalaceae	COUM

Indian paintbrush	*Castilleja*	Mutis ex L. f.	Scrophulariaceae	CASTI2
dalmatian toadflax	*Linaria damatica*	(L.) Mill.	Scrophulariaceae	LIDA
butter and eggs	*Linaria vulgaris*	Mill.	Scrophulariaceae	LIVU2
blue penstemon	*Penstemon cyaneus*	Pennell	Scrophulariaceae	PECY3
violet	*Viola*	L.	Violaceae	VIOLA

Chapter 2: Habitat susceptibility model extension for leafy spurge and rush skeletonweed in the Greater Yellowstone Ecosystem.

Abstract

Habitat distribution models can be used to predict where invasive weeds may occur in order to direct ground surveys and aid in early detection. Land managers facing challenges from invasive plants benefit from habitat susceptibility models because a model can encompass millions of hectares and indicate where time, personnel, and money should be focused. Models incorporate known locations of a target species and environmental variables that influence habitat suitability for the target species. An effective model requires occurrence locations of the invasive species to train and validate the model. When presence of the invasive species is unknown within an essential area and the area is at risk due to the species' prevalence in the surrounding region, it is beneficial to extend a susceptibility model into the essential area. The Greater Yellowstone Ecosystem (GYE) is a priority landscape that has little human disturbance and unique geothermal activity. Protecting the GYE from habitat degradation caused by invasive species is a priority. The objective of this study was to extend susceptibility models for leafy spurge (*Euphorbia esula* L.) and rush skeletonweed (*Chondrilla juncea* L.) from Idaho into 1.12 million ha of the GYE. Environmental variables used were maximum temperature, minimum temperature, sun angle, precipitation, and normalized difference vegetation index (NDVI). Leafy spurge susceptibility encompassed 105,100 ha (9% of the study area) and rush skeletonweed susceptibility encompassed 396,500 ha (33% of the study area). Leafy spurge susceptibility is concentrated along the Yellowstone River north of Gardiner, MT, and into Yellowstone National Park. Rush skeletonweed was predicted to be susceptible in the drainages flowing into Yellowstone River but not along the dry river valley like leafy spurge. Both models show susceptibility in West Yellowstone and around Hebgen Lake. The south-eastern and central portions of the study area, around Lake Yellowstone and Old Faithful, are only predicted to be susceptible to rush skeletonweed. Overall, the study area is at low risk to leafy spurge and rush skeletonweed invasions but as invasive weeds, it is important to closely monitor the area. If populations are discovered within the GYE, susceptibility models could be refined using the new location data to more accurately predict future invasion locations.

INTRODUCTION

Non-native plant invasions threaten the diversity and function of managed and wild systems around the world. In the United States, the control costs and economic loss associated with invasive plants on agriculture yield, wildlife-related recreation, associated flooding, etc. is $35 billion dollars annually (Pimentel et al. 2005). A county weed crew could likely eradicate a rangeland weed on three to six ha given an average, limited budget, while a private landowner would likely only be able to eradicate an infestation on less than two hectares (Zamora and Thill 1999). Infestations larger than 1,000 ha are unlikely to be eradicated, meaning an indefinite financial commitment (Rejmánek and Pitcairn 2002). The most cost-effective approach for managing invasive weeds is through early detection when their spatial extent is small, and eradication is possible (US Congress 1993; DiTomaso 2000; Olliff et al. 2001; Rejmánek and Pitcairn 2002; Lass et al. 2005). Each dollar spent on prevention can avoid 17 dollars needed for ongoing control (US Congress 1993). Propagule presence in suitable habitat allows for establishment therefore, identifying suitable habitat can focus early detection efforts (Wallace and Prather 2016). Early detection is key because the longer an invader is established, the greater the propagule pressure, rate of spread, and cost of control.

Aerial imagery has been used to detect and map populations of invasive species based on unique reflectance values of the invader (Anderson et al. 1993; Lass et al. 2005). While multispectral data is available at 1-m spatial resolution through the National Agriculture Imagery Program (NAIP), 10-m to 30-m spatial resolution is more commonly used (e.g. Sentinel and Landsat) due to greater spectral resolution (hyperspectral), faster processing time, and less storage space needed. However, infestations must be dense monotypic stands of at least 0.1 to 0.5 ha for hyperspectral data alone to identify patches (Lass et al. 2005). If the invader is interspersed among other species it is extremely difficult to develop a unique signature for the invader and the affected area would have to be much larger than a monoculture patch to be detected (Shafii et al. 2004). A surrogate to identifying the target species itself is to identify the associated environmental characteristics indicative of suitable habitat.

Understanding where an invasive species' niche falls along the environmental continuum can direct survey efforts to areas most susceptible to invasion and lend to early detection. Environmental gradients of solar radiation, temperature, and moisture availability are strongly influenced by slope and aspect variations, leading to differences in habitat suitability (Daubenmire 1942). Aspects oriented towards the equator receive greater irradiance and therefore typically experiences warmer temperatures and more evapotranspiration than polar-facing aspects (Holland and Steyn 1975). Steep slopes on equatorial-facing aspects receive more direct irradiance compared to gentle equatorial-facing aspects, the inverse is true on polar-facing aspects. Equatorial-facing aspects offer suitable conditions for species with lower water demand while polar-facing aspects provide conditions for species tolerant to lower levels of sunlight. Environmental variables can be interpreted using a geographic information system to develop habitat distribution models.

Habitat distribution models predict areas susceptible to invasion based on environmental characteristics at known weed infestations (Lass et al. 2011). These types of models have been used for conservation efforts by: identifying suitable habitat of rare species that should be protected (Boetsch, et al. 2003; Ghareghan et al. 2020), locating large infestations of established invasive weeds to be monitored (Lass et al. 2011), and predicting suitable habitat of invasive species to be surveyed for early detection (Wallace and Prather, 2016; Prather et al. 1994). Building a model requires a robust set of known locations of the target species to train the model. A model compares abiotic and biotic factors such as slope, aspect, and vegetation data (spectral data) at known infestations of a target species to a broader area to predict the susceptibility of that area to a specific invasive species. In the case of a susceptibility model, the vegetation data is a surrogate for green vegetation abundance or moisture conditions which are general landscape qualities that can be applied over a larger area than the specific reflectance of a monotypic infestation (Lass et al. 2005). Using remote sensing data to aid in habitat classification to direct field surveys is more cost effective and timely than on-the-ground surveys alone because a model can encompass millions of hectares and prioritize survey locations.

Leafy spurge (*Euphorbia esula* L.) is native to Eurasia and was first reported in the United States in the 1820s, likely introduced from contaminated soil from ship ballasts and crop seed (St. John and Tilley 2014). Leafy spurge is an effective invader because it is tolerant of a wide range of moisture conditions from meadow and riparian communities to mountain ridges and upland sites (USDA Forest Service 2012). Each mature stem produces approximately 140 seeds which are dispersed up to 4.5 meters by explosive seed capsules

(Stevens 1932; Prather et al. 2016). It is present across the southern Canadian provinces and the United States, excluding southern U.S. states (Figure 2.1), and is listed as noxious in 22 states (USDA NRCS 2020). Leafy spurge produces a toxic milky sap that can cause diarrhea and weakness in cattle and horses if consumed. It reduces forage quantity by over 50% because cattle avoid grazing palatable plants in areas that are lightly infested (10% cover) with leafy spurge (Olson 1999). Yellowstone National Park (YNP) listed leafy spurge as a priority 1 weed, indicating its limited presence in the park and urgency for eradication of identified patches (Olliff et al. 2001).

Rush skeletonweed (*Chondrilla juncea* L.*)* is native to Central Asia and the Mediterranean region and was introduced into the United States in the 1870's (Van Vleet and Coombs 2012). Rush skeletonweed infests millions of acres across Washington, Idaho, Oregon, and California. It is present in eastern states and Canadian provinces as well the west (Figure 2.2). Rush skeletonweed overwinters as a rosette and mature plants have wiry stems 0.3-1.2 m tall with a lot of branching. Its wiry branches and milky latex interfere with harvest equipment in agriculture systems. In rangelands, rush skeletonweed reduces forage by out-competing native or beneficial species. It reproduces vegetatively and by seed, with a single plant producing up to 20,000 seeds annually. Rush skeletonweed occurs in needlegrass-sagebrush (*Achnathernum* P. Beauv*/Stipa* L.-*Artemisia* L.) steppe in Russia, Iraq, and eastern Europe (McVean 1966). Rush skeletonweed is on the watch list for YNP, meaning it has either not been documented within park boundaries or was found but removed before seed dispersal (Olliff et al. 2001). The National Park Service (NPS) is required by law to prevent exotic plant introduction and control current infestations (Federal Noxious Weed Act of 1974 [NPS 1996]). The preferred method of control starts with early detection of aggressive invasive plants, focused along roads and developed areas (Olliff et al. 2001).

Yellowstone National Park is at the heart of 8-million rugged and wild hectares comprising the Greater Yellowstone Ecosystem (GYE) (Noss and Cooperrider 1994). The GYE is a host of biological diversity across portions of Montana, Idaho, and Wyoming. Due to minimal human disturbance within the GYE, its natural diversity remains essentially intact (Glick et al. 1991; Noss and Cooperrider 1994). Since 1983 the Greater Yellowstone Coalition (GYC) has worked to protect the ecosystem through active management of water, land, and wildlife. However, invasive weeds across the expansive landscape create challenges for the GYC. Invasive weeds have been introduced from adjacent land by means of human, livestock, and natural vectors (Olliff et al. 2001). The rugged terrain and magnitude of the GYE make ground surveys impractical and unlikely to successfully detect small, new infestations which is why the GYC has decided to incorporate susceptibility models into their management strategy. The GYC is interested in modeling habitats susceptible to leafy spurge and rush skeletonweed invasions because both species are present in Montana and Idaho, adjacent to the GYE (Prather et al. 2016). However, there are limited location data for leafy spurge and rush skeletonweed within the GYE so a specific GYE model would be inaccurate. Leafy spurge and rush skeletonweed location data were well defined for Idaho and the study area in the GYE has similar environmental context as adjacent Idaho. The purpose of this research is to 1) extend current leafy spurge and rush skeletonweed models from Idaho into a portion of the GYE to direct ground surveys and 2) determine what portion of the study area is susceptible to each species.

METHODS

ORIGINAL MODEL DEVELOPMENT

This project was made possible by previous work done at the University of Idaho that incorporated extensive leafy spurge and rush skeletonweed infestation data in southern Idaho to construct habitat susceptibility models. Environmental variables used in model development were normalized difference vegetation index (NDVI), average annual precipitation, maximum temperature, minimum temperature, and sun angle difference. Atmospheric corrected reflectance files from NAIP imagery (National Agriculture Imagery Program), downloaded from USGS EarthExplorer in the form of 3.75 x 3.75-minute quarter quadrangles, were used to calculate NDVI.

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{Red}}{\mathrm{NIR} + \mathrm{Red}}$$

NDVI values were multiplied by 1000 to store data in integer form and reduce computation of exceedingly long decimals. Average annual precipitation, maximum temperature, and minimum temperature data were 30 arc-seconds (~800 m) PRISM grids with 10-m spatial resolution in decimal degrees for 2010 (PRISM Climate Group 2015). Precipitation represents the annual precipitation, in centimeters, for 2010. Temperatures represent the maximum and minimum temperature for 2010. Sun angle difference was the estimated amount of hill still shaded due to slope, aspect, and sun angle, for June 12 (56.6°) at sun azimuth 237° from hill shade of March 12 (23.8°) at sun azimuth 237° (Lass et al. 2011). This variable was created in TerrSet (Clark Labs, Worcester MA) using a digital elevation model (DEM).

Once variables correlated with presence were identified locations of leafy spurge and rush skeletonweed were used to construct signature files (Figure 2.4). Approximately 60% of known locations were used to build the models, known as training sites, and the remaining 40% were used to assess model accuracy, known as validation sites (Lass et al. 2011). The *MakeSig* tool (TerrSet, Clark Labs, Worcester MA) used the environmental variables described above and training sites to create signature files for leafy spurge and rush skeletonweed. Signature files contain the minimum, maximum, mean, and variance within training locations for a variable as well as the covariance between that variable and each other variable. Signature files allow for supervised classification which, classifies landcover based on user-defined classes . The signature files were used in the *MahalClass* tool which determined Mahalanobis Typicality values for each pixel within the study area. *MahalClass* is a soft classifier that identifies the likeness of each pixel to the training sites based on Mahalanobis Typicality values. Mahalanobis Typicality values range from 0 to 1.0, larger values indicate more similarity to the training locations while smaller values represent less similarity to training locations. Mahalanobis Typicality values were used to group pixels into three susceptibility categories—low, moderate and high, plus a not susceptible category. Specific values for each species are presented below.

EXTENDING MODELS

To extend the leafy spurge and rush skeletonweed habitat susceptibility models, the same environmental variables used in the original models were downloaded for the new study area. NAIP data were downloaded for 1.12 million ha, bounding coordinates of: 110°8’9” W, 111°16’26” W, 44°10’55” N, 45°22’34” N. Those bounding coordinates encompass most of Yellowstone National Park (YNP). The eastern edge of the study area is 10 km west of the eastern boarder of YNP, west to Hebgen Lake in Montana. The northern border is 38 km north of Gardiner, MT, and continues south to 6 km from the southern border of the park. The red and near-infrared (NIR) spectral bands from the National Agriculture Imagery Program (NAIP) were downloaded from USGS EarthExplorer in the form of 3.75 x 3.75-minute quarter quadrangles. Given the latitude of the study area, each quarter quad was roughly 3,200 hectares. Approximately 220 quarter quads were downloaded then mosaiced together in longitudinal strips for processing.

Idaho, Montana, and Wyoming NAIP images showed changes to spectral bands as borders were crossed and required adjustments to bring values to similar ranges across state boundaries. Habitat susceptibility models were created for Idaho and so Montana and Wyoming images were calibrated to Idaho values. Several histograms were used on sample areas to determine the maximum, minimum, and mean values for each state then a calibration was applied to adjust values, 1.732 and 1.592 for Montana and Wyoming respectively. Although Sentinel-2 imagery were uniform across state boundaries and easier to process, NAIP data were used to extend habitat susceptibility models for GYE because NAIP were used for signature values in the original models.

The maximum temperature, minimum temperature, sun angle, and precipitation data used in the original model encompassed the GYE study area, so the GYE study area was extracted from each dataset using the *Window* tool in TerrSet (TerrSet v. 18.31, Clark Labs, Worcester, MA). The signature files created for each species in southern Idaho were used to calculate susceptibility in the GYE. Each layer used to create the original signature file was named within the file so the classification process would use the proper files (Figure 2.5). The signature file that identified the layers within the new study area was used in the *MahalClass* tool in TerrSet.

Susceptibility for invasion within the distribution models was divided into three categories and an additional zero category to indicate no susceptibility. The low, moderate, and high susceptibility categories were based on Mahalanobis Typicality values from the *MahalClass* tool. The Mahalanobis Typicality value for the not susceptibility to leafy spurge category was set from 0 to < 0.003, low susceptibility to leafy spurge was 0.003 to < 0.40, moderate was 0.40 to <0.80, and high was 0.80 to 1.0. Rush skeletonweed categories were 0.0 to <0.005, 0.005 to < 0.40, 0.40 to <0.80, and 0.80 to 1.0 for zero, low, moderate, and high susceptibility, respectively. Data from the Greater Yellowstone Coordinating Committee

(GYCC), Northern Rocky Mountain Exotic Plant Management Team, YNP Exotic Plant Management Team, and the US Forest Service contained few leafy spurge locations and they were not within a susceptibility category, so the low category was set to include some of those locations. There were no location data for rush skeletonweed in the study area.

RESULTS

Signature files indicated the biggest differences between rush skeletonweed and leafy spurge were the range of annual precipitation and NDVI. The mean precipitation for rush skeletonweed was 32.3 cm with a range of 7 to 63 cm. Leafy spurge precipitation ranged from 7 to 55 cm with a mean of 25.5 cm. NDVI reflectance range for rush skeletonweed was 0.155 to 0.903 with a mean of 0.623 compared to the range of leafy spurge of 0.943 to 0.888 and a mean of 0.555. Sun angle difference encompassed the full range of the variable, -100 to 100, and their average values were similar, 45 for rush skeletonweed and 46 for leafy spurge. Temperature ranges also were similar. For rush skeletonweed maximum temperature ranged from 6.7°C to 19.4°C with a mean of 12.6°C and minimum temperatures were -7.2°C to 5.0°C with a mean of -1.4°C. For leafy spurge maximum temperatures ranged from 7.8°C to 18.9°C with a mean of 13.0°C and minimum temperatures were -6.7°C to 4.4°C with a mean of -2°C.

Leafy spurge susceptibility encompassed less than 9% of the study area; 103,700 ha. Only 2 ha were predicted in high susceptibility, 1,400 ha predicted in moderate susceptibility, and the remaining 103,700 ha were in low susceptibility (Table 2.2). Most of the susceptible habitat was along the Yellowstone River, from north of Gardiner, Montana south in to YNP. There also is susceptible habitat near West Yellowstone, MT, and around Hebgen Lake.

None of the study area was predicted to be highly susceptible to rush skeletonweed. Rush skeletonweed susceptibility covered 33% of the study area, 300 ha in moderate susceptibility and 396,500 ha in low susceptibility (Table 2). Rush skeletonweed susceptible habitat occurred in the drainages that flow into the Yellowstone River but not in the dry river valley like leafy spurge. Susceptible habitat also was prevalent south of Lake Yellowstone and to the northwest around Old Faithful and Madison Campground in YNP. Susceptibility continued west to Hebgen Lake and south into Idaho. Susceptible habitat of each model appears to be most influenced by precipitation (Figure 2.6 and Figure 2.7).

DISCUSSION

The GYE is an intact ecosystem with a diverse flora that needs to be protected from invasive weeds (Noss and Cooperrider 1994; Olliff et al. 2001). Early detection is the most cost-effective approach to weed eradication if infestations are found when the spatial extent is small (<1,000 ha) (US Congress 1993; Rejmánek and Pitcairn 2002). In this study we extended susceptibility models for leafy spurge and rush skeletonweed from southern Idaho into 1.12 million ha of the GYE to determine the risk of invasion by these two species and to direct ground surveys for early detection. Leafy spurge susceptibility covered less than 9% of the study area and rush skeletonweed susceptibility covered 33% of the study area. These models greatly reduced the area needed to be surveyed, saving land managers time and money.

Rush skeletonweed is known to invade needlegrass-sagebrush steppe communities (McVean 1966) which are similar to up to 52,000 ha of *Artemisia* spp. habitat types within YNP (Despain 1990). If rush skeletonweed moves into sagebrush steppe habitats in the YNP and throughout the GYE, it could have devastating impacts on herbivores and the fire regime (USDA 2014). Fortunately, rush skeletonweed has only been documented in three counties within 100 km of the study area, Madison and Bonneville counties in Idaho and Sublette county, Wyoming (USDA, NRCS 2020). Keeping rush skeletonweed populations contained in those counties and preventing satellite populations from establishing in the GYE should be a priority.

Although rush skeletonweed susceptibility is predicted across more of the study area than leafy spurge, leafy spurge poses an immediate threat, as it has been documented in all counties within and adjacent to the study area (USDA, NRCS 2020). Leafy spurge has the potential to be more devastating across the landscape due to its ability to infest riparian zones (USDA Forest Service 2012). Riparian systems represent a small percentage of any landscape but provide essential functions such as sediment filtration, flood control and habitat connectivity (Seavy et al. 2009). Typically, riparian systems are resilient to invaders but human disturbance, such as agriculture or development, can create openings for invasive plants. The agriculture north of Gardiner, MT, represents the largest area of leafy spurge susceptibility within the study area. The Yellowstone River flows north out of YNP at Gardiner, MT, fortuitously keeping seeds from dispersing into the park via water, from adjacent agriculture land. Though, northern portions of the GYE along the Yellowstone River are at risk to water dispersed propagules. The south western portion of the study area that is susceptible to leafy spurge is along the Warm River and in adjacent forests and shrublands. This area presents a greater challenge because it is remote, has multiple small drainages and only has one road that moves along the leafy spurge susceptible habitat. Survey efforts need to be extensive and thorough because an infestation in this area could expand unnoticed.

Suitable habitat within the GYE study area indicates future invasion of leafy spurge and rush skeletonweed is possible. While habitat distribution models cannot be constructed in areas with sparse location data, extending habitat distribution models from other areas allows risk of invasion to be evaluated for the target invasive plant species. Remote sensing data within a GIS allow landscape level assessments of conditions that may be suitable to invasive weeds, but data can pose challenges. Discrepancies between states and the number of NAIP quarter-quads needed to cover the study area created uncertainty in interpretation. NAIP data are typically collected by state, and different states may be mapped using different sensors (Maxwell et al. 2017). Projects that encompass multiple states risk inconsistencies in imagery due to varying radiometric properties of sensors. Over 200 quarter-quads were needed for the GYE study area. Because NAIP imagery are collected by airplanes instead of satellites, the time it takes to capture images across a large area can result in differences in shadow size and direction. Mosaicking hundreds of tiles together can create marginal errors across the study area. NAIP is best suited for single state projects.

Future work for modeling habitat susceptibility to invasion from invasive plant species will rely on the ability to use models developed in adjacent areas when the invasive plant species is limited in distribution within the area of interest (GYE in this case). While extending models has potential for prediction error within the area of interest, those errors can be addressed as survey begins and data are acquired through ground survey to modify models within the area of interest.

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Figure 2.1 Leafy spurge distribution

Figure 2.2 Rush skeletonweed distribution

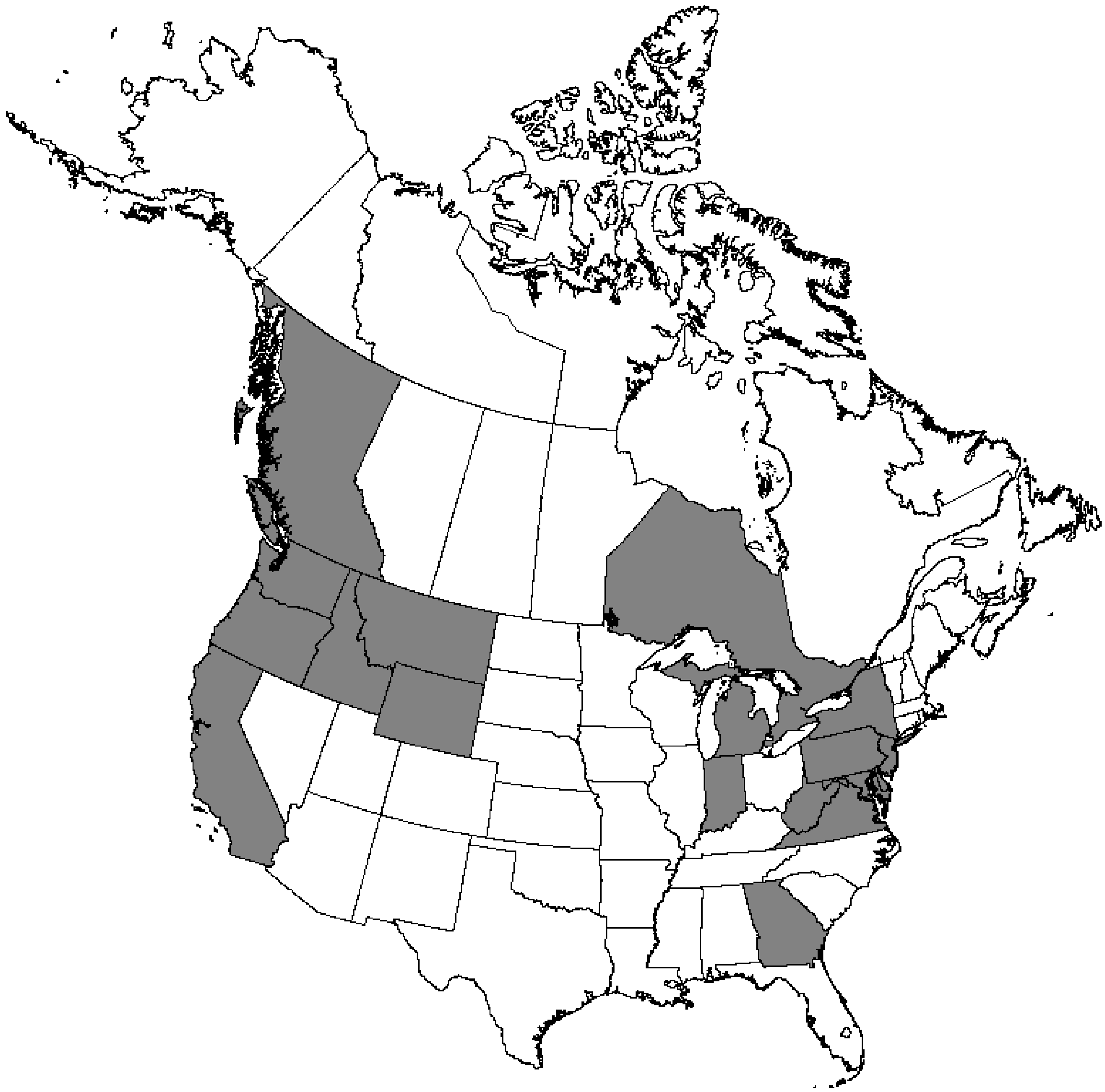


Figure 2.3 Study area within the Greater Yellowstone Ecosystem

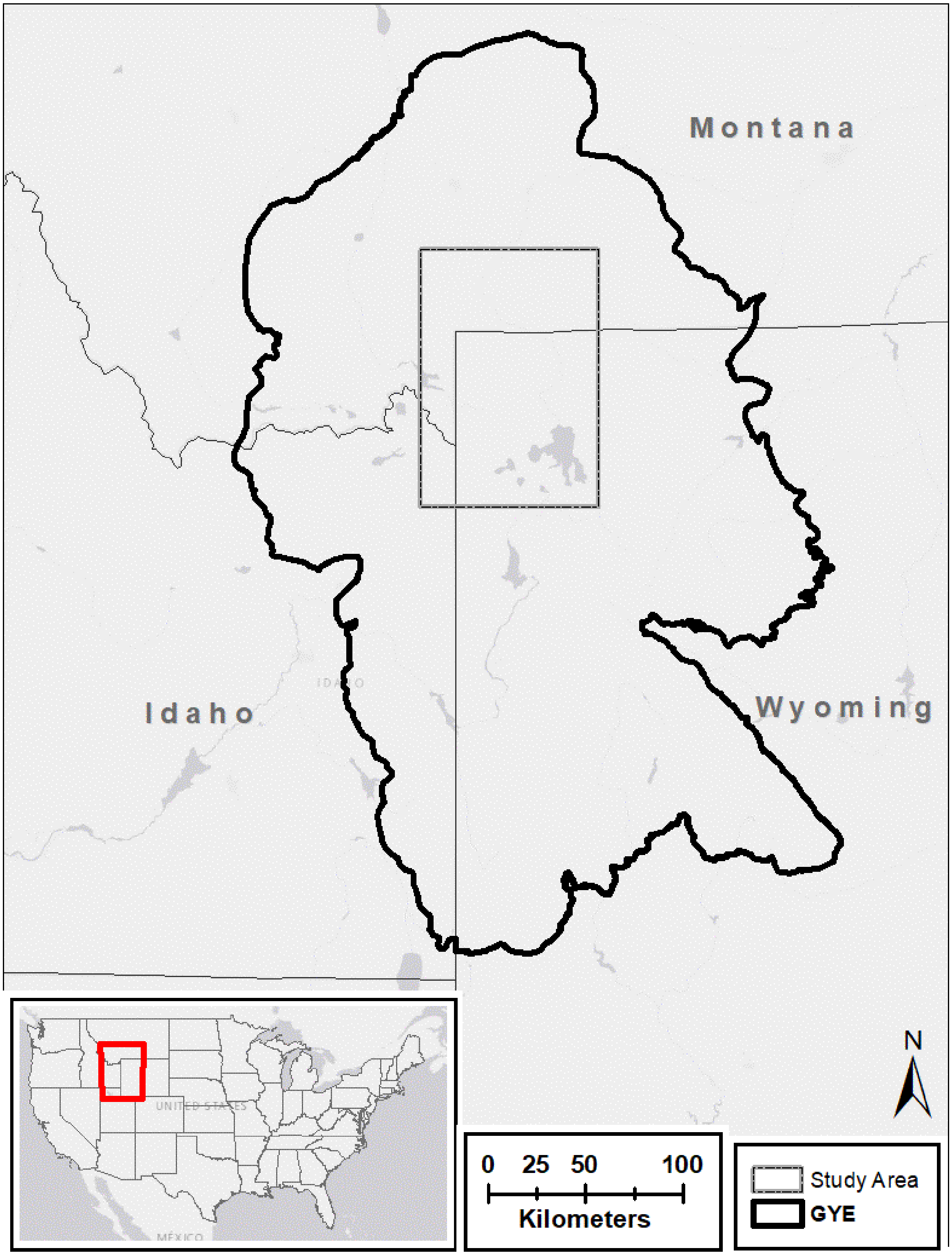
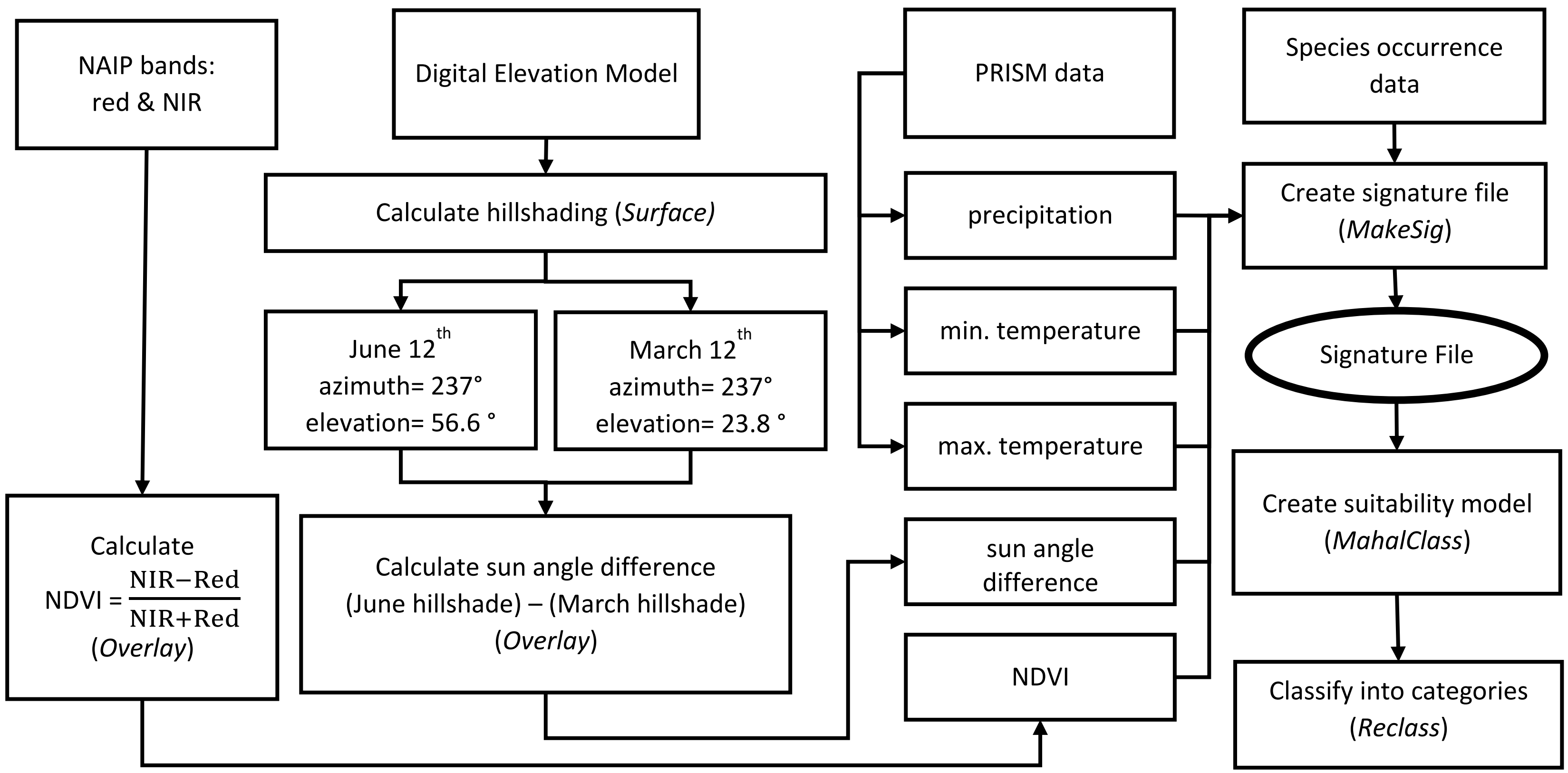


Figure 2.4 Steps to create susceptibility model using environmental data and species occurrence locations. Words in *italics* indicate TerrSet tools.



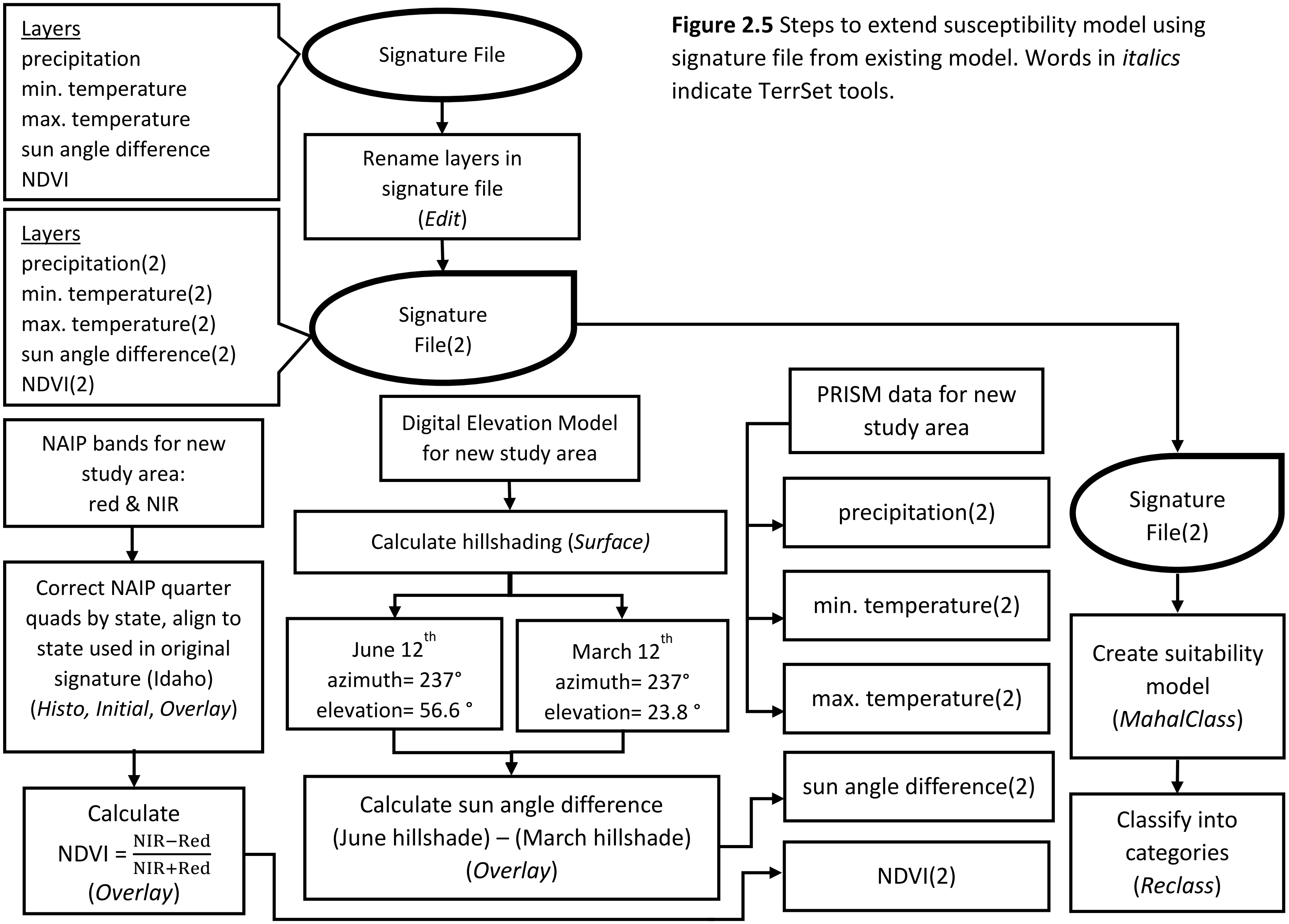


Figure 2.5 Steps to extend susceptibility model using signature file from existing model. Words in *italics* indicate TerrSet tools.

Figure 2.6 Rush skeletonweed susceptibility (A) and precipitation map (B). Rush skeletonweed susceptibility is closely associated with precipitation between 11 cm and 34 cm, occasionally up to 44 cm.

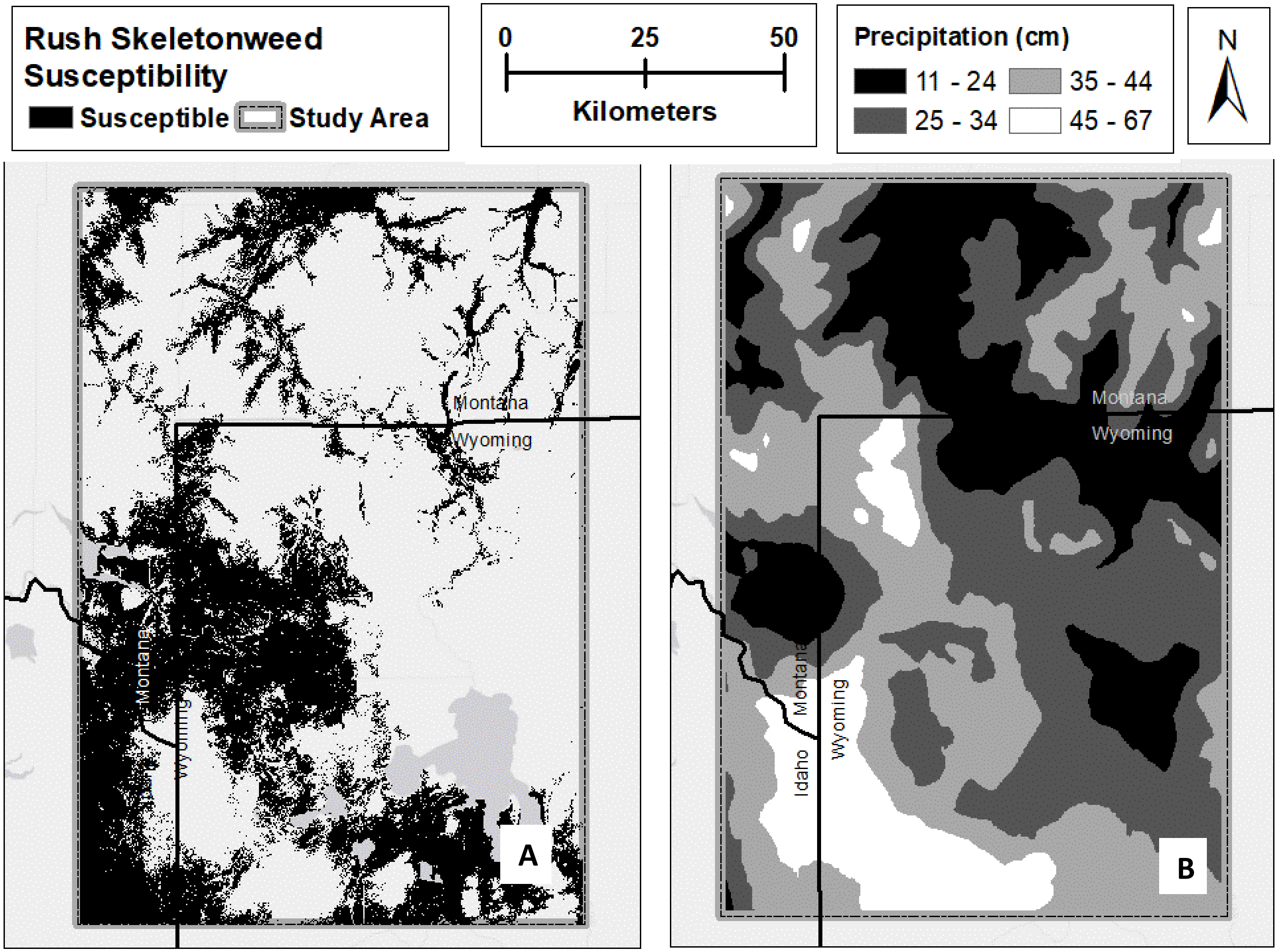


Figure 2.7 Leafy spurge susceptibility (A) and precipitation map (B). Leafy spurge susceptibility is primarily within the lowest precipitation range, 11-24 cm, but ocassionally from 25-34 cm in the south west corner of the study area.

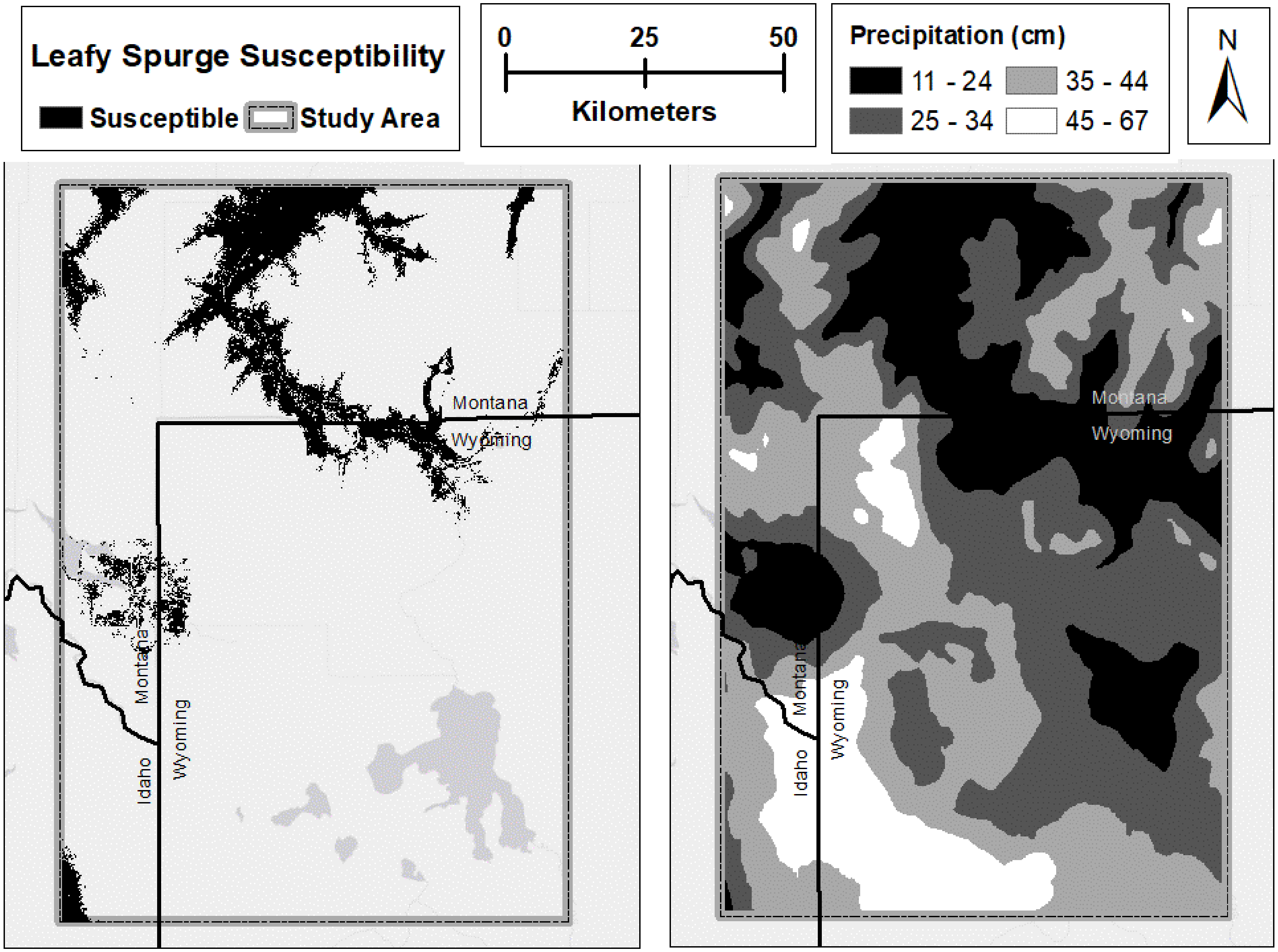


Table 2.1 Leafy spurge susceptibility categories

Susceptibility categories	Mahalanobis Typicality Values	Percent of Study Area	Total Hectares
not susceptible	$0.0 < x < 0.003$	91.2	1,093,200
low	$0.003 < x < 0.40$	8.7	103,700
moderate	$0.40 < x < 0.70$	0.1	1,400
high	$0.70 < x \leq 1.00$	0.0	2

Table 2.2 Rush skeletonweed susceptibility categories

Susceptibility categories	Mahalanobis Typicality Values	Percent of Study Area	Total Hectares
not susceptible	0.0 $< x <$ 0.005	66.9	801,500
low	0.005 $< x <$ 0.40	33.1	396,500
moderate	0.40 $< x <$ 0.70	0.0	300
high	0.70 $< x \leq$ 1.00	0.0	0