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Research Article

Unearthing the habitat of a hyperaccumulator: case study of the invasive plant yellowtuft (*Alyssum*; Brassicaceae) in Southwest Oregon, USA

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Abstract

Invasive species pose a critical risk to wildlife habitat, ecosystem processes, and agricultural productivity. This risk is exemplified by the spread of Yellowtuft (*Alyssum murale* and *Alyssum corsicum*), in Josephine County, Oregon. Both species have spread into protected botanical areas, which are home to a number of endemic and endangered species. ArcGIS 10 software suite, a comprehensive system used to collect, analyze and distribute geographic information, provided the platform for spatial analysis of infestation sites. The advanced statistical model, MaxEnt, was used to project the likely distribution and suitable habitat for Yellowtuft across 208,513 hectares of southern Oregon and northern California, and identify patterns of spread and habitat suitability. 12 environmental characteristics representing topography, climate, soil characteristics and vegetation cover were used to project distribution across the study area. Current infestations were not found to exclusively reside along spread pathways - roads and streams – or require serpentine soils to establish. The single most important variable related to habitat suitability was elevation, followed by slope, soil depth and vegetation cover class. The suitable map identifies 10,729 hectares as suitable habitat for both *Alyssum* species, with the vast majority residing within the Illinois River Valley. The final results were overlaid with the 2011 surveyed areas to identify areas that were of high suitability but not yet surveyed to identify survey gaps and possible areas to focus treatment effort for the 2012 and 2013 field season. The results were also overlaid with a prospective aerial survey flight plan to examine if the survey incorporates all areas of high suitability. With limited resources, and costly efforts like aerial surveying, species modeling and spatial analysis provided information that assisted managers to streamline efforts and identify areas of higher suitability that were not actively surveyed.

Key words: MaxEnt; phytomining; modelling; noxious weeds; *Alyssum murale*; *Alyssum corsicum*; eradication; habitat suitability

Introduction

Invasive species pose a continuous threat to economic interests and ecological systems throughout the world (Blossey 1999). In the United States, the financial cost from crop and natural resources revenue loss and ongoing treatment efforts ranges anywhere from $100-200 billion annually (Schnase et al. 2002). The spread of invasive species has resulted in reduction of wildlife habitat, degradation of natural ecosystems, alteration of ecological processes, and an overall decline in productivity (Davies and Sheley 2007). Two new invaders, *Alyssum murale* and *Alyssum corsicum,* in Josephine County Oregon, USA, have emerged as the state's most critical invasive species concern.

Alyssum murale and *A. corsicum* are perennial forbs native to the Mediterranean region and southern Europe and have been documented as thriving in similar soil and environmental conditions (Li et al. 2003; Broadhurst et al. 2004). *A. murale* grows as tall as 1 meter, and is covered with gray green oval shaped leaves. *A. corsicum* is similar in size and appearance, although the leaves have a more pronounced oval shape and are covered with a dense layer of silvery hairs (Amsberry et al. 2008). *A. murale* and *A. corsicum* produce clusters of small brightly colored yellow flowers, leading to the shared common name of Yellowtuft. Both species shed most of their leaves prior to going to flower in early summer, making it nearly impossible to visually distinguish one from the other (Amsberry et al. 2008). One unique characteristic they share is that both species are nickel hyperaccumulators, a trait only shared with about 300 other plant species in the world. These specialist plants accumulate nickel in concentrations greater than 10,000 micrograms per gram of dry weight (µg/g dry weight) (Brooks 1998) compared to the 0.01–3.0 µg/g dry weight found in most plants. Toxic effects occur in non-hyperaccumulating plants when nickel exceeds 50-100 µg/g dry weight (Angle and Linacre 2005).

In the late 1990's, both species were imported into Oregon to investigate usage in an alternative mining technique called phytomining. Phytomining is an experimental mining technique in which hyperaccumulating plants are used to mine soils that are otherwise too costly or labor prohibitive to mine (Anderson et al. 1999). In 2002, an alternative mining company, Viridian Inc., began leasing fields in and around Cave Junction and started planting *A. murale* and *A. corsicum* for commercial purposes. This area is comprised primarily of serpentine parent rocks and soil, which are naturally high in heavy metals including nickel (Strittholt and Dellasala 2001). This soil type, coupled with a temperate Mediterranean climate, resembled the native habitat of both species and made the Cave Junction area a seemingly ideal place to investigate nickel phytomining from a commercial standpoint. At the time of importation, research scientists assumed the plants were unable to germinate in undisturbed soils and required soils with high concentrations of heavy metals to establish and spread (Amsberry et al. 2008). It is unclear if a formal assessment of spread or impact risk was ever completed prior to introduction for research purposes and whether consideration of the abundant serpentine soils in the area and the delicate ecological impacts of spread were considered. Concerns of spread were voiced by local land managers and residents after the planted fields were established. Those concerns were realized in 2005 when several "escape" sites were discovered far outside the initially planted fields (Amsberry et al. 2008).

The exact dispersal mechanism for unintended spread of the *Alyssum* species is not known. Little information is available about seed dispersal of either species in their native habitat, and the same can be said for the newly invaded area. Both species produce hundreds of small papery seeds during each growing period. Once the plant stems senesce, seeds fall to ground below the plant, or are carried on the senesced stems and dispersed. Several newly emerging seedlings have been found at the base of local shrubs, and the dried stalks of the previous year's plant are stuck in the shrub's branches. Wind is a likely mechanism for seed dispersal and could disperse the seeds over a narrow or wide range depending on the amount and type of obstacles (fences, shrubs, tall grasses, and water). During laboratory observation, the flat papery *Alyssum* seeds germinated after sitting in a petri dish of water for a few days (Amsberry et al. 2008). This may be an indication that the seeds remain viable even when submerged in water and could disperse to new sites via waterways. It is unlikely that seeds are dispersed by animals, given the toxicity of the plants and subsequent seeds (Boyd 2004). However, no formal research has been conducted on seed dispersal, seed viability or growth for either *Alyssum* species at the date of this publication.

Escaped *A. murale* and *A. corsicum* have been found within the boundaries of two protected botanical areas, Rough and Ready Flat and Eight Dollar Mountain. Dense infestations of a hundred plants or more have been found outside of the planted fields, creating small monocultures of both species (Amsberry et al. 2008). This is of major concern to both public land managers and local citizens given the unique biodiversity of the area. The entire area falls within the EPA level three ecoregion: Klamath Mountain/California High North Coast Range (Sleeter and Calzia 2011). The Klamath Mountain region is one of the world's biodiversity "hotspots," and includes more than 3,500 plant species, 200 endemic species, and 27 species of conifers (Myers et al. 2000; Sleeter and Calzia 2011). The large outcroppings of serpentine soil in and around Cave Junction are home to 70 endemic species. Two species in this area are federal listed endangered species and an additional 15 have a conservation status by either state and/or federal agencies. If allowed to spread, the *Alyssum* species could potentially overwhelm vulnerable endemic species by monopolizing scarce resources.

Other ecological concerns include an increase in the likelihood of metal toxicity to animals and insects grazing on the plants, and the increased concentration of nickel below plants after leaf senescence (Boyd 2004). The redistribution of metal concentrations to the base of the plants has been characterized as elemental allelopathy in which the *Alyssum* plants change the soil around them and create a less suitable habitat for other plant species (Zhang et al. 2005, Morris et al. 2009). While this theory is still being explored, the redistribution and concentration of metals due to the presence of *A. murale* and *A. corsicum* is a major concern for land managers.

Current management strategy

Managers consider a number of strategies for invasive species, including no action, containment, control, and eradication. Managers chose an eradication strategy for the Josephine County *Alyssum* infestation for two primary reasons: the potential impact of unconstrained spread, and the multiple agency and public support for aggressive action. The potential for loss of endemic and protected species provides the greatest justification for a strong eradication policy (Rejmanek and Pitcarin 2002). Efforts to eradicate large infestations of other invasive plants have been successful, but have required a large financial commitment and extended hours of on-the-ground treatment activities (Rejmanek and Pitcarin 2002). At present, both species are under quarantine, which limits the introduction of outside seeds to the area and the total infested areas is relatively small and lightly populated. The limited potential for re-introduction from outside the area, and the size of the infested area (less than 1% cover over 30,000 hectares) are positive indications that eradication can be successful (Simberloff 2003; Rejmanek and Pitcarin 2002). To implement an eradication strategy, managers must first establish a surveillance method to determine the extent of the infestation. Surveillance is generally based on a manager's understanding of species behavior, the results of on-the-ground or aerial surveys to show species distribution, cost-benefit analyses of survey methodologies, and local politics that may influence treatment priorities.

Statement of problem and project objectives

The purpose of this work is to advance the efforts to eradicate *A. murale* and *A. corsicum* by improving the surveillance strategy using both documented and potential plant spread. The major management questions addressed include: Are there distinguishable trends related to spread that can inform better surveillance? Are there particular areas that are more or less suitable for *A. murale* and *A. corsicum*? How can managers update surveillance strategies as they gain more information overtime?

The specific objectives are to:

1. Determine which environmental characteristics are strongly correlated with the local establishment of either *Alyssum* species, to gain a better understanding of these species in this new environment;
2. Identify individual sites within the broader geographic area that are of high likelihood for infestation (Areas that have a greater than random likelihood of providing suitable habitat);
3. Compare the predicted suitable habitat to the 2011 field surveys and the proposed aerial survey to identify places that are highly suitable for both species but have not been scheduled for surveying during the 2012 field season;
4. Provide suggestions for future analysis of the landscape and incorporation of other mechanistic or process-based models, in order to provide management with an easy-to-use, quantitative measure of the spread of the invasion.

Study area

The study area for this project is approximately 208,513 hectares, covering Josephine County, OR, and small portions of Jackson County in Southern Oregon and Del Norte County in California (Figure 1). The study area has a Mediterranean climate, consisting of hot dry summers and mild wet winters (Sleeter and Calzia 2011). The area is comprised of Jeffrey pine and Douglas fir forests, intermixed with outcroppings of rocky outcroppings (Damschen et al. 2010). The climatic variation and complex soil composition provides a multitude of habitat niches.

Methods

Survey points

Occurrence data for *A. murale* and *A. corsicum* were collected over a period of six years from 2005–2011. The surveys were conducted by the US Forest Service, Oregon Department of Agriculture weed technicians, and trained volunteers. Infestation data did not distinguish definitively which species was found at each surveyed site. Many infestations contained a mix of both species, and land managers have approached them as a single target species. For this reason, the survey points for occurrence are representative of both species and were modeled together. In total, 627 single infestation points were used as presence data. These points were recorded as a UTM coordinate from the central location of the infestation. The actual infestation density varied between sites, some sites contained a single plant and others contained a thousand or more plants. The infestations of *Alyssum* are patchy in both size and percent of area covered. For the purpose of this research, each point represents a single infested area.

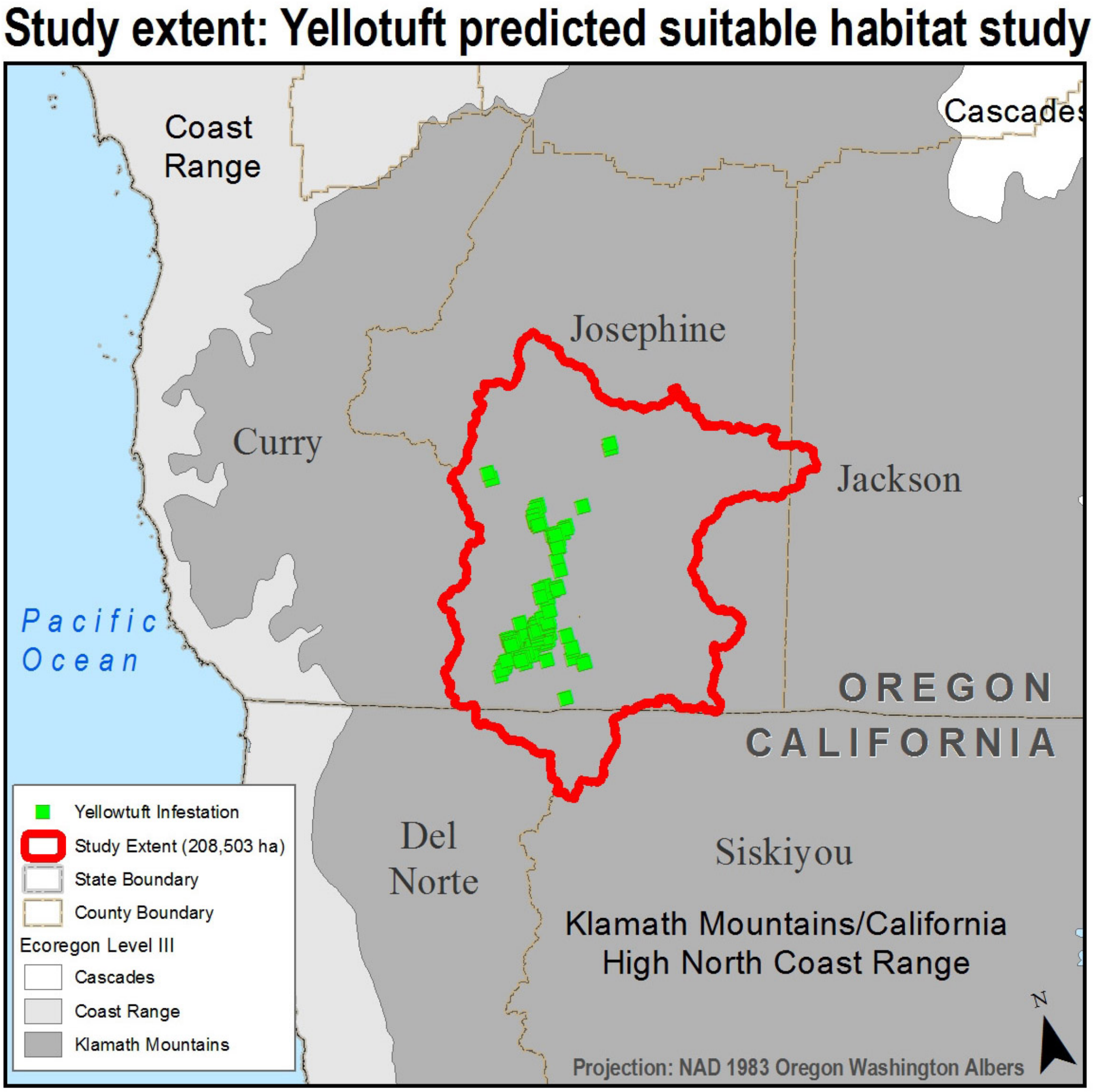

Figure 1. Study area for the habitat suitability model covering portions of Southern Oregon and Northern California.

The survey points that fell within the initially planted fields were excluded from the survey point dataset to ensure that the evaluation was based on the suitability for naturally spreading plants. The final 627 survey points were used in spatial analysis. The 627 were then applied to a grid matching the cell size and location of the environmental variable datasets below. Duplicate sites were removed so that only a single site fell within occupied cells. This process resulted in 322 individual survey points used in the species distribution model.

Environmental variables

The establishment and spread of any plant species is intrinsically linked to the availability of resources (water, nutrients, sunlight), the general structure of the landscape (e.g., soil type, slope, temperature), and the proximity to dispersal pathways (e.g., roads, streams). Three different groups of environmental variables were selected for analysis: climatic, topographic, and edaphic (soil characteristics). Each group expresses a different type of environmental gradient – direct or indirect – that influences resource gradients across a landscape (Guisan and Zimmermann 2000). Two climate datasets were downloaded from the PRISM climate group (http://www.prism.oregonstate.edu): average annual precipitation, average annual minimum temperature. Both spatial datasets were rescaled to 100-meter resolution to match the spatial scale of the soil dataset. All spatial analyses were conducted using ArcMap 10 and the Spatial Analyst tools.

Three topographic variables were generated and used in the final model: slope, aspect, and elevation. Each variable has been used in predictive vegetation modeling (Franklin 1995; Hirzel et al. 2002). A 10-meter Digital Elevation Model (DEM) original generated from *The National Map* created by the United States Geological Survey (http://nationalmap.gov/index.html) was downloaded, and clipped to the study area boundary. Slope and aspect raster datasets were created from this DEM. Last, all data layers were converted to ASCII grid format for use in the MaxEnt distribution model.

Soil variables were estimated using the Natural Resources Conservation Service's Soil Survey Geographic (SSURGO) database (http://soildatamart.nrcs.usda.gov/) (Arnold et al. 2004). The variables used in this study include: soil pH, cation exchange capacity (CEC), available water capacity (AWC), drainage class, serpentine soil, and depth to soil restrictive layer (soil depth). The serpentine soil layer was generated from the SSURGO soil survey's parent material layer. Parent material refers to the rock or organic material from which soil is derived. All areas with parent material comprised of serpentinite, perioditite and/or ultramafic rocks were selected (Kruckeburg 2006). A total of 17,169 hectares – approximately 8 percent – of the study area does not have a completed soil survey. The soil data for these areas was interpolated through a method called ordinary kriging, using the Spatial Analyst toolbox in ArcMap 10 (ESRI, Redlands, CA, USA). Kriging is a geostatistical process that assumes the distance and/or direction between several specified points can explain variation between those points, and thus generate data for the space between those points. Kriging is a common interpolation method for both soil and geologic datasets (Zhu and Lin 2010). The kriging model utilized the 30 closest points in circular radius to interpolate missing values. The serpentine layer was used in the Spatial Analysis but was not included in the species distribution model.

Three additional variables related to distance from distribution pathways or originating seed source were included. The first is distance from a stream or river which was generated using ArcGIS Spatial Analyst toolset and a linear feature dataset of streams and rivers supplied by the US Forest Service. The second dataset is distance from a road, generated from a linear feature displaying roads data supplied by the US Forest Service. Last, a spatial layer of the planted fields was supplied by the US Forest Service and Oregon Department of Agriculture.

Spatial analysis

A central question of this analysis is whether the species are exclusively following waterways or roads, since method of spread dictates surveillance, control and eradication strategies in part. Proximity to the initially planted fields is also a major consideration as they are the point of initial seed source for the entire infestation. Another consideration is the connection between establishment and serpentine soils, since restriction to the latter could potentially limit further spread in the area. Spatial data layers for rivers and roadways were acquired from the Rogue River Siskiyou National Forest. The number of infestations within 100 meters of roads, streams and planted fields, was calculated, along with the number of survey sites that fell on serpentine soil. This process provided information about the current location of sites and some general information about spread limitations in this environment.

Statistical distribution, model choice and description

MaxEnt is a multiple purpose model that can be used with presence-only data in scenarios where little physiological information is known about the target species. It is considered a multiple purpose model because it has been used for a wide range of species (plants, animals, diseases) under a variety of scenarios (endemic species, climate change scenarios, and invasive species) (Elith et al. 2011). Several studies comparing MaxEnt to other presence-only models have reported consistently accurate results (Elith et al. 2006; Evangelista et al. 2008; Moreno et al. 2011; Hoffman et al. 2008). The method is founded on the maximum-entropy principle articulated by Jaynes (1957). Jaynes argued that the unknown distribution of a species is best approximated when we incorporate any known constraints (environmental variables), and subject to those constraints, the distribution should display maximum entropy (Jaynes 1957). In the MaxEnt modeling environment, entropy is a measure of how scattered or dispersed a species can be across a given landscape (Elith et al. 2011). I used MaxEnt version 3.3.3k (http://www.cs.princeton.edu/~schapire/maxent/).

MaxEnt calculates the probability that a species, in this case the two *Alyssum* species, could establish and/or persist at a particular location within a defined landscape. For each environmental variable, a numerical value was supplied for each cell. From the entire landscape, 10,000 sample 100 meter cells were randomly selected and utilized to create a background dataset. This allowed for a representative sample of the environmental variation across the study area without substantially slowing model performance (Phillips 2006). A second set of values, referred to as the "training" data, was calculated for cells in which a plant was present. A separate selection of presence sites were removed and used as "test" data to compare with the model created from the training data. Three hundred and fifty three cells were available as presence sites, 242 were randomly selected as training data, and 80 were randomly selected as test data.

MaxEnt averaged the background environmental variables and then fit the training data's environmental variables to the background data to create the final model. During the model processing, the gain of the model was calculated for both the overall model and for each environmental variable. The "gain" of the model is a numerical value for the overall goodness-of-fit, comparable to deviance (Philips 2006). The process was completed for each individual environmental variable to assess how much of a contribution each variable made to the overall goodness-of-fit of the model. If the model gain was equal to 2.5, then the average likelihood for presence sample (exp (2.5) = 12.182) was 12.182 times higher than a random background pixel (Philips 2006). Further explanation of this equation can be found in the MaxEnt tutorial available at http://www.cs.princeton.edu/~schapire/maxent/ .

Three model versions, each with differing regularization values (0.5, 1. and 1.5), were generated and compared to determine which model best predicts *Alyssum* species suitable habitat. The regularization value changes how tightly the output results are distributed. A value of greater than 1 is more widely distributed, and a value less than 0.5 will generate a tighter distribution. Each model was submitted to ten replications, each time creating a new random sample for the background dataset, training data, and test data. An index was created quantifying the ratio of predicted presence-to-expected presence (Hirzel et al. 2006). The index provides a way to evaluate consistency in the model outputs, determining which of the three model versions is best, and a reference for reclassifying the modeled outputs into two classes, suitable and non-suitable (Hirzel et al 2006). The average ratio for all 10 replications is used to generate a spearman's rank correlation. Spearman's rank correlation generates a value between -1 to 1, with positive values indicating greater consistency between the predicted distribution and the distribution of the occurrence dataset. Accuracy of the model was evaluated using the area under the curve (AUC) of the receiver-operating characteristic curve (ROC), and comparison of the training gain to the test gain (Wang et al. 2010). The AUC is expressed as a value between 0 and 1, with a perfectly random model having a value of 0.5. The closer the AUC value is to one, the more consistent the model is at predicting presence when performing cross validation (Stohlgren et al. 2010). To estimate the importance of each individual environmental variable, a jackknife test was performed on the model gain of the test data.

Results

Spatial analysis of infestation location and serpentine soil revealed that a majority of infestation sites were found to reside on serpentine soils with 383 of the 627 known infestation sites falling on serpentine soils. The spatial analysis of infestations to roads, streams and planted fields indicated that currently invaded sites are not exclusively proximate to roads, streams or the originally planted fields (Table 1). 170 of the 627 known *Alyssum* infestation sites fell within 100 meters of a road (27%). The remaining 457, nearly 73 percent of all sites, were located further than 100 meters from a road. Of the total study area, 34,172 hectares (16%) fell within 100 meter of roads. Similarly, a relatively small percentage of infestation sites fell within100 meters of streams, approximately 244 of the 627 infestations (39%). The remaining 383, approximately 61 percent, of infestations sites were beyond 100 meters of a stream. Nearly half of the study area, 101,237 hectares (48%), fell within 100 meters of a stream. Proximity to the planted fields had the lowest number of sites within 100 meters with 107 infestations. The remaining 520 sites, almost 83 percent, were further than 100 meters from the planted fields.

Table 1. Proximity of *Alyssum* infestations to roads, streams and the initially planted fields.

Distance from pathway/seed source	Roads		Streams		Planted Fields	
	# of sites	(%)	# of sites	(%)	# of sites	(%)
< 20	115	18.34%	77	12.28%	34	5.42%
20 - 40	20	3.19%	64	10.21%	33	5.26%
40 - 60	13	2.07%	48	7.66%	22	3.51%
60 - 80	3	0.48%	42	6.70%	10	1.59%
80 - 100	19	3.03%	24	3.83%	8	1.28%
> 100	457	72.89%	372	59.33%	520	82.93%

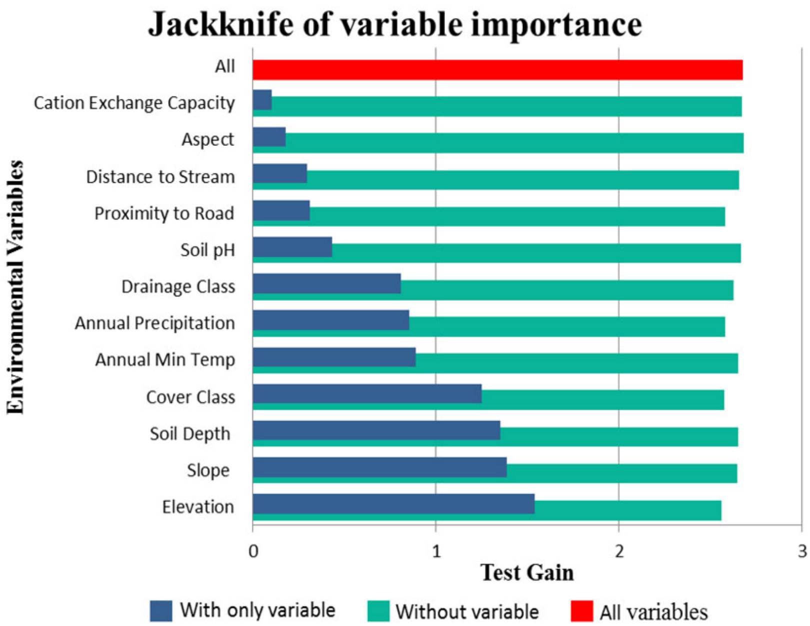

Figure 2. Jackknife test of individual variable importance related to the model final model gain. The dark blue lines represents the test gain with only the specified environmental variable. The teal line represents the model gain with all the environment variables except the indicated environmental variable. A reduction, of teal line indicates the amount of information provided by that variable that is not provided by another environmental variable.

The model generated with all 12 environmental variables, and calibrated with a regularized multiplier value of 0.5, was selected as the final model. The model had a very high accuracy measure with an average test AUC of 0.975, ± 0.002. The high test AUC indicates that the model is highly accurate (Wang et al. 2010). The final model had an average regularized test gain of 2.676, indicating the model has a high fit to the presence samples and an omission rate of 0.0378. The Boyce Index revealed that the final model had a greater number of species occurrence in areas identified as having a relatively higher suitability, with a strong Spearman correlation value of 0.998.

The jackknife test examining each variable in isolation revealed that the most important variables in their contribution to model gain were elevation, slope, soil depth, cover class, average annual precipitation, and annual minimum temperature (Figure 2). The second part of the jackknife test evaluated how much of the information provided by each individual variable was compensated by the other variables. There was very little change in the predictive accuracy when any single variable was excluded from the model. Three variables that showed the biggest decrease was elevation, cover class, and distance to a road indicating that some of the information pertaining to these three variables was not provided by any of the other variables.

A spatial layer was created that displayed a prediction percentage for each one-hectare cell across the entire study area (Figure 3). Less than

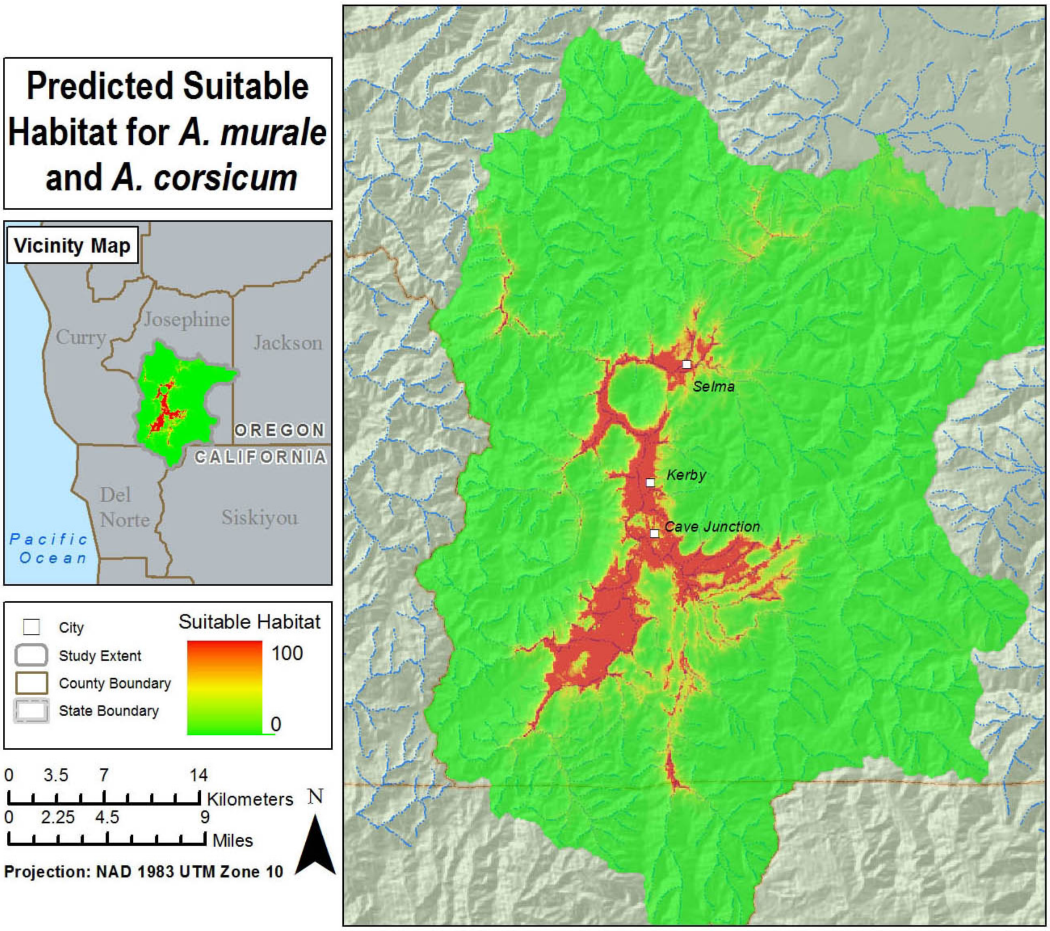

Figure 3. Predicted suitable habitat for *A. murale* and *A. corsicum* within study boundary. Warm colors indicate higher suitability, and cool colors indicate less suitable conditions.

ten percent (approximately 10,729 ha) displayed a greater than random likelihood of *Alyssum* establishment. The vast majority of this area falls directly in the Illinois River Valley, with a higher likelihood in the area surrounding the Illinois Valley airport, a smaller area on the west side of highway 199 north of Cave Junction, and around the base of the Eight Dollar Mountain Botanical Area.

Discussion

Spatial examination of current infestation locations contradicts previous assumptions about the environmental conditions needed for germination and growth of these species in the natural environment (Amsberry et al. 2008). One assumption is that both *Alyssum* species are dependent on serpentine soils to establish successfully and spread (Ghaderian et al. 2007). Angel and Linacre (2005) suggest the *Alyssum* species, which have evolved on heavy metal soils, tend to be less resistant to bacteria and fungus occurring in non-serpentine soils, thus they are confined to serpentine soils. However, Analysis on presence data showed that over 39 percent of the infestations occur on non-serpentine soils and appear to be unrestrained by soil type. This result is also contrary to one page risk analysis written in 2003 that indicated *A. murale* needed heavy metal soils in order to establish and spread (Roseburg 2003). Additional studies have also documented the high accumulation and growth of *A. murale* and *A. corsicum* on a variety of soil types (Li et al.

2003; Broadhurst et al. 2004). Seeds for both species were able to germinate in a range of nickel concentrated soils in both greenhouse trials and outdoor study sites (Li et al. 2003; Broadhurst et al 2004; Psaras et al. 2000). These studies validate the patterns of growth and spread of *Alyssum* in Josephine County documented in this study. One caveat to these findings is the scale and accuracy of the soil datasets utilized in the analysis. Field studies of associated species and soil composition are needed to validate this analysis. However, the potential ease of spread into multiple soil types should be a major consideration and concern when contemplating future phytomining operations utilizing these two plants and others given the potential for rapid evolution in invading plant species.

The majority of infestations were not found within close proximity to either roads or streams, contrary to what surveillance teams reported. This analysis indicates that surveillance along streams should cover areas to a100-meter buffer from the stream bank and beyond. While forty percent of sites falling within 100-meters is a high percentage overall, the area itself constitutes nearly half the entire study area. That leaves an additional sixty percent of sites that could be missed if crews do not extend the surveys beyond the 100 meter buffer. In comparison, 27% of sites were within the 100-meter buffer of a road even though that area accounts for only 16 percent of entire study area. The results indicate that the 2012 surveys should not focus efforts solely on areas along roads and streams to best ensure that not a single infestation site is missed. Furthermore it illustrates the need for ongoing spatial analysis to examine whether or not trends observed in the fields are supported by the data. A successful eradication effort requires the identification and treatment or removal of all plants, requiring a comprehensive strategy for surveillance.

The predicted presence layer generated from the final MaxEnt model provided some encouraging information for land managers working to eradicate these species. A small portion of the entire study area had a high likelihood of presence for either *Alyssum* species. The predicted area was almost exclusively within the Illinois River Valley, extending outward along the riverbanks heading northwest around the base of Eight Dollar Mountain. The vast majority of predicted habitat followed the observed infestation distribution. However, a few areas with similar habitat were located just northeast of the valley, where two infestations were found in the summer of 2011. There is one isolated area in Siskiyou County, California that has a suitable habitat for the *Alyssum* species. Managers should inspect this isolated site, even though it is unlikely that this area is currently infested given the distance from known infestations. Given these results, the area of the Illinois River Valley has a distinctly different environmental composition and characterization compared to the rest of the study area. Management efforts prior to full eradication should focus on containing the infestation within the valley and eliminating "satellite" infestations from seeding down river.

To date, the *Alyssum* species have not had the opportunity to invade all habitat types within the study area. MaxEnt results presented are provisional and represent a snapshot of the spread to date, and can be interpreted as the preferable habitat under a limited spatial and temporal range. The occurrence date utilized may also present some bias to the model given that they were record as part of management surveying. Surveying with the intent of using the information for modeling requires systematic sampling across the entire landscape. Surveys were limited in some cases by access to land, topographic barriers, and the perception that new infestations would be clustered around existing infestations. Consequently, current study predictions should be interpreted knowing that all potential habitats have not been surveyed and the predicted distribution reflects survey efforts as of fall 2012. Finally, presence-only models do not account for the prevalence or density of a species on the landscape which can bias results (Elith et al. 2011). The model does not rank the sites with 1,000 individual plants higher than sites with a single plant. It is clear that a high density of plants may be a result of an area being more suitable then others.

Future considerations for research and management

While this study addresses biotic and abiotic environmental factors that affect plant establishment and reproduction, specific dispersal mechanisms for these two species were not examined, in part because little information is available about specific mechanism of spread. Measuring or estimating the potential dispersal rate was not possible in this study given that the majority of surveys completed prior to 2011 did not document what date the plant was found, or if it was at a new site or an existing site. Recording the date the infestation was surveyed each year, and if it is new or regrowth from the previous year, should be included in surveys starting during the field season of 2012. By capturing that temporal component which had been missing in previous surveys, it would be possible to model mechanisms for dispersal and rates of spread. Modeling dispersal mechanism and spread rates would provide information about the *Alyssum* plants that can be used in concert with the habitat suitability model. Combined these two pieces of information will help managers form a better surveillance and treatment strategy.

Conclusion

The coupling of spatial datasets with advanced modeling and GIS mapping software can greatly inform management of spread patterns, available habitat, and gaps in current invasive plants across all forest service regions and administrative levels. The information generated from modeling complements the on-the-ground efforts and informs the on-the-ground treatment efforts for the 2012 and 2013 field season. For example, the results of this study indicate a few isolated suitable habitat sites outside of the larger suitable habitat area (Figure 3). Survey crews should focus on these isolated, or satellite sites, for early detection of infestations. This along with focusing efforts on the edges of the infestations would focus efforts on the outer most perimeter of the infestation. Treatment can start at this point and work toward the center of the infestation, hopefully resulting in eradication. Throughout this process it is critical that the newly gathered survey data be integrated into the modeling process, along with field observation, and newly available research.

The introduction, escape and spread of *A. murale* and *A. corsicum* has been aptly characterized as the "perfect storm" invasive species scenario. The unique ability of these species to thrive in what was considered an "un-invadable" habitat and the potential irreversible impacts to the area's unique ecosystem have created a sense of urgency among land managers and local interest groups. However, plans for eradication have been complicated by a lack of cooperation with some members of the public and limited knowledge of the plants' growth and spread. Success of this effort hinges on the ability of representatives from all agencies and organizations to organize around a single strategy, informed by field observations and advanced spatial analysis.

The coupling of spatial datasets with advanced modeling and GIS mapping software can greatly inform management of spread patterns, available habitat, and gaps in current invasive plants across all forest service regions and administrative levels. The information generated from modeling complements the on-the-ground efforts and inform the on-the-ground treatment efforts. For example, the results of this study indicate a few isolated suitable habitat sites outside of the larger suitable habitat area (Figure 3). Survey crews should focus on these isolated, or satellite sites, for early detection of infestations. Surveying satellite sites and the perimeter of the infestations would focus efforts while allow managers to first contain the spread. Treatment can start at this point and work toward the center of the infestation, hopefully resulting in the eradication of both species. Throughout this process it is critical that the newly gathered survey data be integrated into the modeling process, along with field observation, and newly available research.

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