12-2011

Using Species Distribution Models to Assess Invasion Theory and Provide Management Recommendations for Riparian Areas in the Eastern Columbia and Western Missouri River Basins

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Recommended Citation

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USING SPECIES DISTRIBUTION MODELS TO ASSESS INVASION THEORY AND PROVIDE MANAGEMENT RECOMMENDATIONS FOR RIPARIAN AREAS IN THE EASTERN COLUMBIA AND WESTERN MISSOURI RIVER BASINS

by

Diane R. Menuz

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Karin M. Kettenring Major Professor	Charles P. Hawkins Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

2011

ABSTRACT

Using Species Distribution Models to Assess Invasion Theory and Provide Management Recommendations for Riparian Areas in the Eastern Columbia and Western Missouri River Basins

by

Diane R. Menuz, Master of Science

Utah State University, 2011

Major Professor: Dr. Karin M. Kettenring
Program: Ecology

Invasive plant species impact ecosystems by altering native plant community composition and modifying ecosystem properties such as fire and nutrient cycles. We used species distribution models to address both theoretical and applied questions regarding invasive plants in an ecosystem particularly vulnerable to invasion, riparian areas. In our first study, we asked whether a native species is closer to equilibrium than a functionally similar invasive species and determined drivers of invasion for an aggressive invader of riparian areas, *Phalaris arundinacea* (reed canarygrass). We modeled the presence of *P. arundinacea* and a comparable native species using four techniques and compared model fit between species and between models with and without dispersal processes incorporated. Non-dispersal model fit for our invasive species was lower than for the native species and improvement in fit with the addition of the dispersal constraint was greater for the invasive species than the native species. These results provide evidence that invasive species are further from equilibrium than native species and suggest that dispersal processes should be considered when modeling invasive species. In our second study, we addressed whether there was a set of site traits that make some sites more prone to invasion by non-native plants than others. We used Random Forests to individually model the presence of 11 invasive plant species that are designated as noxious weeds in our study area. We used model results to identify general patterns of invasion and to provide management recommendations for the study area. We found that a particular site type was more likely to be invaded by the majority of study species: hot, dry sites with high grass or shrub cover near roads with high nutrient levels and high stream baseflow values. Management recommendations to combat invasion by *P. arundinacea* in particular and invasive species in general are the same: limiting species' spread along roads, lowering site nutrient levels, and anticipating increased spread with climate change.

(100 pages)

PUBLIC ABSTRACT

Diane Menuz

Globalization has created opportunities for plant and animal species to be transported to novel ecosystems. A subset of these species become invasive species, which are able to persist and spread rapidly to become influential components in their new ecosystems. Invasive species are often able to out-compete co-occurring native species and can alter fundamental ecosystem properties, such as soil nutrient availability or time between wildfires in a region. The United States is estimated to lose $34 billion per year to invasive plant species through costs to control unwanted species and lowered crop and forage production.

We used statistical models to better understand invasive plant species in our study region, the eastern Columbia and western Missouri river basins. These models, referred to as species distribution models, relate site attributes, such as proximity to roads or climatic conditions, to the presence or absence of the species of interest. One assumption of these models is that species are absent from sites for reasons that can be captured by predictor variables, such as cold temperatures or too little rain, rather than by the species' inability to disperse to the sites. Our first objective was to determine whether models performed better at predicting the presence of native species than the presence of invasive species since the latter have had limited time to spread in the area where they have been introduced. We also wanted to determine whether including a measure of the distance to nearby sites occupied by the focal invasive species increased model performance by capturing some of the regional dispersal potential. In our second study, we modeled the distributions of 11 plant species designated as noxious weeds by state regulatory agencies within our study area. Our objective was to determine the site attributes most frequently associated with invasion so we could make recommendations for management action to lower invasion risk in our study area.

We found that model performance was lower for the invasive species than for the native species and that including a measure of nearby occupied sites increased performance more for the invasive species than for the native species. We recommend that researchers consider dispersal limitations as part of their species distribution modeling process. Our results may improve the ability of distribution models to accurately predict invaded areas. In our second study, we found a particular site type that was more likely to be invaded by the majority of study species: hot, dry sites with high grass or shrub cover near roads with high soil nutrient levels and fluctuating stream water levels. Monitoring efforts should focus on sites that fit this description. Management actions that may limit invasion include limiting species' spread on roads, adjusting soil nutrient levels to favor native species over invasive species, and preparing for increased invasion with climate change. Research results will be shared with the Forest Service Rocky Mountain Research Station to be disseminated to land managers in our study region. Project results should help lower the rate of spread of invasive species and make species' control efforts more cost effective by focusing on the most vulnerable sites.

ACKNOWLEDGMENTS

Funding for this research was provided by the S.J. Quinney Masters Fellowship at Utah State University and the USDA Forest Service Fish and Aquatic Ecology Unit. Many former and current members of the PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program out of the Forest Service Rocky Mountain Research Station in Logan, UT provided data support and project feedback, including Ryan Lokteff, Andrew Hill, Peter Ebertowski, Caroline Laine, Dr. Brett Roper, and Eric Archer. John Olson and Ryan Hill provided substantial GIS support and together with the rest of the laboratory of Dr. Charles Hawkins provided constructive advice that led to substantial improvement of the second chapter. Dr. Susan Galatowitsch provided useful commentary about habitat relationships for *Phalaris arundinacea*. Members of the Kettenring laboratory, especially Lexine Long, Nate Hough-Snee, Eric Hazelton, and Amanda Sweetman, helped improve the third chapter.

Friends and family provided support and kept me sane throughout my master’s experience, especially my parents and my sister. And, finally, the members of my committee provided exceptional support and helpful feedback throughout this process. Dr. Richard Cutler and Dr. Charles Hawkins always made time to answer my questions and helped me have the confidence to pursue the questions I found interesting. Dr. Karin Kettenring, my major professor, kept me focused, provided encouragement, and read each chapter almost as many times as I did. Thank you.

Diane R. Menuz

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CHAPTER 1

INTRODUCTION TO BIOLOGICAL INVASION IN RIPARIAN AREAS, SPECIES DISTRIBUTIONS MODELS, AND STUDY QUESTIONS

Invasive plant species cause substantial economic and ecological harm throughout the world (Simberloff 2001). Biological invasion occurs when a species rapidly becomes a dominant component of a community where it was not found previously, either because the species is introduced to a new environment or because environmental conditions are altered in such a way that the species is at a competitive advantage (Valery et al. 2008). We limit the term invasive species to species not native to a particular area. Invasive plant species are estimated to cost the United States at least $34 billion per year (Pimentel, Zuniga & Morrison 2005) and almost half of the imperiled species in the United States are threatened by invasive species (Wilcove et al. 1998). Invasive plant species can dramatically alter ecosystems; for example, studies have found that invasive plant species can decrease native plant and invertebrate species diversity (Gerber et al. 2008), change nutrient availability (Ehrenfeld 2003), and alter disturbance regimes including fire cycles (Mack & D'Antonio 1998).

Riparian areas are particularly vulnerable to invasive plant species due to both high potential for ecological harm and high susceptibility to invasion. Riparian vegetation plays an important role in determining nutrient levels, sedimentation processes, bank stability, and water temperatures in adjacent streams (Richardson et al. 2007). Riparian vegetation also supports high levels of terrestrial biodiversity (Poff et al. 2011). Changes in riparian vegetation via plant invasion can lead to changes in stream and terrestrial functioning (Tickner et al. 2001; Gerber et al. 2008; Urgenson, Reichard & Halpern

2009). Riparian areas are often found to be more heavily invaded than adjacent upland areas (DeFerrari & Naiman 1994; Stohlgren et al. 1998; Hood & Naiman 2000). Invasion may occur in part because streams can act as dispersal corridors, carrying propagules to downstream habitat once a species is introduced locally (Johansson, Nilsson & Nilsson 1996; Tabacchi et al. 2005). Flood events can further aid invasion by opening up resources such as space and light that allow species to establish (Pysek & Prach 1993; Parendes & Jones 2000). Management tools for dealing with invasive species in riparian areas are critically needed.

Species distribution models can be an important tool for combating invasive species (Peterson 2003). These models build a statistical relationship between the presence of a focal species and underlying environmental conditions at sites where the species is found. For invasive species, these models can help prioritize sites for monitoring and control efforts by predicting areas that are most likely to be invaded. For example, Hoffman et al. (2008) created maps of the potential distributions of five invasive plant species along the North Platte River and found that susceptibility was higher in the eastern part of the river. Distribution models can also be used to identify factors that promote invasion, leading to management recommendations. For instance, Loo (2009) found that the aquatic invasive grass *Glyceria maxima* in Australia is associated with high soil nutrient content which suggests that site nutrient management may help limit spread of this species.

In this thesis, we addressed both theoretical and applied aspects of invasion ecology using species distribution models. We used riparian vegetation data from streams in the eastern Columbia and western Missouri river basins for analysis. In Chapter 2, we evaluated the extent to which species distribution models are appropriate for modeling invasive species and then used the results to better understand factors associated with invasion by the riparian invader *Phalaris arundinacea* L. (reed canarygrass). Species distribution models assume that modeled species are at equilibrium with their environment (Elith & Leathwick 2009). This may not be true for invasive species because they have had limited time to spread throughout their introduced range. Recent work has incorporated measures of dispersal potential into distribution models of invasive species to account for this problem (Allouche et al. 2008; Václavík & Meentemeyer 2009). However, it is unknown if the issue of non-equilibrium is more of a problem for invasive species than for native species. We compared model accuracy of distribution models with and without a dispersal constraint for the invasive riparian plant *P. arundinacea* and the functionally similar native *Calamagrostis canadensis* to evaluate whether the invasive species appears to violate the assumption of equilibrium. We also used the models to better understand factors related to invasion by *P. arundinacea* because of this species' recognized importance as a threat to riparian and wetland areas (Galatowitsch, Anderson & Ascher 1999; Lavergne & Molofsky 2004). We identified drivers of invasion at the landscape scale for this species in order to inform management decisions and new experimental research.

In Chapter 3, we looked at what makes some sites more susceptible to invasion than other sites. A variety of characteristics have been linked to site invasibility, including changing fire regimes (Keeley, 2006), novel grazing pressure (Diez et al. 2009), and natural or anthropogenic differences in nutrient levels (Bakker & Berendse 1999; Maron & Jefferies 1999). An understanding of these characteristics can help prioritize areas for monitoring and control efforts and determine appropriate management actions to lower site invasion risk (Hobbs & Humphries 1995; Pyšek & Richardson 2010). Much of the previous work on the relationship between site characteristics and invasion risk has looked at only one or a few invasive species (Evangelista et al. 2008; Ibáñez et al. 2009b; Loo et al. 2009), looked at only one or a few factors related to invasion (Wilson et al. 1992; Matthews et al. 2009), or modeled richness and/or abundance of all exotic species as a function of site attributes (Ohlemüller, Walker & Wilson 2006, Ibáñez et al. 2009a; Catford et al. 2011). In contrast to this previous work, we used species distribution models to look both at generalities associated with site invasibility and species-specific habitat relationships. We modeled species individually and then looked for a region-wide pattern to determine if site characteristics associated with invasion were conserved across a suite of species. We modeled the distributions of 11 invasive plant species along riparian areas in the northwestern United States using Random Forests. Variables related to climate, disturbance, nutrient and soil conditions, land cover, and site hydrology were included in the models. Model results informed both invasion theory as well as provided management advice for the study region.

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CHAPTER 2

DO DISPERSAL CONSTRAINTS IMPROVE SPECIES DISTRIBUTION MODELS? TESTS WITH AN INVASIVE AND NATIVE RIPARIAN PLANT SPECIES

Summary

1. Species distribution models assume that modeled species are at equilibrium with their environment. Introduced invasive species may frequently violate this assumption because they have had limited time to disperse to all suitable habitat within their introduced range. Recently, some researchers used measures of dispersal potential in species distribution models to account for this problem. However, their work has not explicitly determined if the issue of non-equilibrium is more of a problem for invasive species than for native species.

2. We compared the accuracy of an ensemble of distribution models with and without a variable accounting for dispersal constraints for the invasive riparian plant *Phalaris arundinacea* and the functionally similar native *Calamagrostis canadensis* to evaluate whether the invasive species violates the assumption of equilibrium. We also used the models to understand factors related to *P. arundinacea* invasion because of this species' recognized importance as a threat to riparian and wetland areas.

3. We predicted that (1) models without dispersal constraints would fit the native species better than the invasive species and (2) the addition of dispersal constraints would improve fit for the invasive species more than fit for the native species. We used logistic regression, classification trees, Random Forests, and Boosted Trees to model distributions and used two accuracy metrics to evaluate model fit.

4. Both of our predictions were validated: (1) model fit was higher for the native species in models without dispersal constraints and (2) incorporation of dispersal constraints improved fit more for the invasive species than the native species. *Phalaris arundinacea* was associated with warm sites that were drier in winter and wetter in summer. Presence was also higher at ungrazed sites with high nitrogen levels near roads.

5. *Synthesis and applications*. Invasive plant species appear to be less likely to meet the distribution modeling assumption of equilibrium than native species. Including dispersal processes in distribution models should increase their utility for managing invasive species. Model results indicate that climate change preparation, nutrient management, and road monitoring will help lower site susceptibility to *P. arundinacea* invasion.

Introduction

Species distribution models are an important tool for understanding landscape-level patterns of invasion (Peterson 2003). These models use environmental variables from surveyed sites to build statistical relationships between those variables and the presence of the species of interest. They can be used to identify factors associated with invasion such as high soil nutrient levels (Loo et al. 2009), low forest cover (Allen & Shea 2006), or areas of high human population density (Nielsen, Hartvig & Kollmann 2008). Distribution models can also inform monitoring and control efforts by generating predictions of areas most vulnerable to invasion (Hoffman et al. 2008; Jarnevich & Reynolds 2011).

A major assumption of species distribution models is that modeled species are at equilibrium with their environment (Elith & Leathwick 2009). This means that species are limited by environmental variables such as climate or soil conditions, rather than by dispersal ability. Invasive species may frequently violate this assumption because they have had limited time to disperse to all suitable habitat within their introduced range (Václavík & Meentemeyer 2009). Recently, researchers have proposed incorporating a measure of dispersal potential into distribution models of invasive species to address this issue and improve model fit (Allouche et al. 2008; Dullinger et al. 2009; Václavík & Meentemeyer 2009). These dispersal constraints are a function of each site's proximity to known occupied sites and serve as an estimate of nearby propagule pressure. Previous research has focused on improving model fit for invasive species without considering the extent to which the problem of non-equilibrium also exists for native species. Here, we compare accuracy of distribution models with and without dispersal constraints for the introduced invasive plant species *Phalaris arundinacea* L. (reed canary grass) and the functionally similar native species, *Calamagrostis canadensis* (Michx.) P. Beauv. (bluejoint) to assess the importance of dispersal constraints for model fit. This approach allows us to evaluate if non-equilibrium is an issue of specific concern for invasive species or is more general to models of all species.

We use riparian areas in the northwestern United States as our study region. Riparian vegetation both provides habitat for terrestrial animals (Poff et al. 2011) and regulates in-stream processes (Richardson et al. 2007). Riparian areas are subject to high levels of anthropogenic disturbance (Goodwin, Hawkins & Kershner 1997), which can be accompanied by accidental or intentional introduction of new species. Frequent natural disturbance via flooding can further exacerbate invasion potential (Parendes & Jones 2000). Plant invasion in riparian areas can alter vegetation composition and thus both terrestrial and stream functioning (Richardson et al. 2007).

We chose *P. arundinacea* as our model invasive species because of its recognized importance as a threat to riparian and wetland areas and because of its use as a model system for the study of biological invasions (Galatowitsch, Anderson & Ascher 1999; Lavergne & Molofsky 2004). This species can lower native plant diversity (Green & Galatowitsch 2002; Werner & Zedler 2002), lower native diversity of some insect groups (Hansen & Castelle 1999) and change sedimentation patterns and hydrologic processes of invaded streams (Lavergne & Molofsky 2004). Researchers have studied *P. arundinacea* extensively in experimental settings to examine how light availability, flood levels, nutrients, grazing, and sedimentation affect its establishment, growth and competitive abilities (Green & Galatowitsch 2002; Maurer & Zedler 2002; Kercher & Zedler 2004; Perry & Galatowitsch 2004) and to compare the effectiveness of different control methods and restoration practices on limiting its spread (Kilbride & Paveglio 1999; Adams & Galatowitsch 2006). Much less work has investigated larger-scale patterns of *P. arundinacea* invasion, and these studies have focused on one or a few drivers of invasion, such as dams and reservoirs (Rood, Braatne & Goater 2010), general disturbance (Ringold, Magee & Peck 2008), land cover (Jakubowski, Casler & Jackson 2010), or nutrients and urbanization (Matthews et al. 2009). Besides the study by Ringold, Magee and Peck (2008), which covered the western United States, these studies were confined to single river systems or portions of individual states. In contrast to previous work, in this study we examined a wide range of factors controlling the distribution of *P. arundinacea* across a large section of the western United States. Such landscape-level work is important for identifying potential drivers of invasion that could inform new experimental research and provide management recommendations.

The objectives of our study were to 1) determine if dispersal processes are more important for models of invasive species than native species and 2) understand factors that regulate the distribution of *P. arundinacea*. To address our first objective, we compared fit for models of *P. arundinacea* and *C. canadensis* with and without dispersal constraints. We predicted that 1) models without dispersal constraints would fit the native species better than the invasive species because invasive species are less at equilibrium with their environment and 2) incorporating dispersal constraints would improve fit for the model of the invasive species and have minimal effect on the model of the native species. We used an ensemble of distribution models to address our second objective to determine natural and anthropogenic drivers of *P. arundinacea.* Our results provide a better understanding of when non-equilibrium needs to be considered for distribution modeling as well as management recommendations for an aggressive invasive riparian plant species.

Methods

Study Species

Phalaris arundinacea is a rhizomatous grass species that is predominantly found in wetland or riparian areas (http://plants.usda.gov). It has been repeatedly introduced to North America from Europe for erosion control and cattle feed, with the earliest introductions in the mid-1800s (Lavergne & Molofsky 2004). We selected the native grass species *C. canadensis* for model comparison because this species' dispersal mechanisms and functional role are similar to *P. arundinacea*. Both species occur throughout the United States and Canada, almost exclusively in wetland and riparian areas (http://plants.usda.gov). They both reach about 1.5 m in height and can regenerate vegetatively with rhizomes and with seeds, with seed dispersal considered an important component of spread (http://www.invasive.org/weedcd/pdfs/tncweeds/phalaru.pdf, Lieffers, Macdonald & Hogg 1993). Based on seed weight and lack of other dispersal characteristics, dispersal for both species is probably primarily through wind or unassisted (Hughes et al. 1994). Some dispersal may also occur through animal ingestion, adhesion to animals via mud, or in streams (Balgooyen & Moe 1973; Vivian-Smith & Stiles 1994; Boedeltje et al. 2004). However, water dispersal is probably not the primary means of *P. arundinacea* dispersal because its seeds have a relatively short float time (Coops & Velde 1995) and lower germination rates when stored in wet versus dry conditions (Comes, Bruns & Kelley). Information about *C. canadensis* water dispersal potential is not available.

Distribution data and study region

We used species distribution data from the U.S. Forest Service's (FS) PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program (PIBO) (Henderson et al. 2005). PIBO collects data on riparian vegetation on FS and Bureau of Land Management (BLM) land in the eastern Columbia and western Missouri River Basins along 80 to 500-m long stream segments (Fig. 2.1). This area encompasses a diverse range of vegetation, including dry forest (*Pseudotsuga menziesii*, *Pinus ponderosa* and *Abies* spp.), cold forest (*Tsuga mertensiana*, *Pinus albicaulis, Pinus contorta* and *Larix lyallii*) and dry shrub (*Purshia tridentata*, *Artemisia tridentata*, and *Juniperus* spp.) (Quigley & Arbelbide 1997). A small portion of the study area is in the northwestern Great Plains. Each stream segment, or site, will be visited at least once every five years, though currently most sites have not had repeat surveys. Vegetation data at each site are collected from a variable number of 20-cm x 50-cm Daubenmire quadrats placed along the greenline, the first place upslope from the stream with at least 25% perennial plant cover. We used data from the first 40 quadrats at each site to maintain a standard number of samples. We considered a species present at a site if it was found in at least one quadrat during at least one PIBO survey between 2003 and 2009. There were a total of 1146 sites in the Columbia River Basin and 193 sites in the Missouri River Basin used in our study.

Predictor variables

We identified 20 non- or weakly correlated (Pearson correlations <|0.70|) environmental variables that represent climatic, land cover, disturbance, hydrological, and soil factors expected to be important to the distribution of plant species (Table 2.1). Data extraction was conducted in ArcMap 10 and Geospatial Modelling Environment 0.5.2 (www.spatialecology.com/gme). We extracted 30-year mean climate values from PRISM (Daly et al. 2008) including mean precipitation of the driest month of the year, mean precipitation of the wettest month of the year, mean temperature of the coldest month of the year, mean temperature of the warmest month of the year, and mean number of days per year between the first and last freeze. Distance to the nearest road and density of roads in a 1-km buffer around sites were calculated from TIGER/lines shapefiles (U.S. Census Bureau 2009) or FS or BLM road data (unpublished data), depending on data accuracy at each site. We used FS and BLM spatial data on grazing allotments (unpublished data) to calculate the presence/absence of grazing allotments at sites and the percent of 1-km buffers around sites that contain grazing allotments. We used fire perimeter data from Monitoring Trends in Burn Severity to create a categorical variable to distinguish between burned and unburned sites for sites that were burned within 10 years of the most recent PIBO survey (Eidenshink et al. 2007). We included two measures of hydraulic conditions at sites: slope and baseflow. Stream segment slope, which is positively related to flood intensity, was calculated from 30-m DEMs (Gesch et al. 2009). Baseflow, the percentage of total stream flow that comes from groundwater discharge, was extracted from USGS Base-flow Index Grid (Wolock 2003). Cover of forest, shrubland, grassland, and other (e.g. development, agriculture, standing water) was calculated in 200-m buffers around each site, based on data from a national vegetation map (LANDFIRE National Existing Vegetation Type layer from U.S. Department of the Interior, Geologic Survey, http://gisdata.usgs.net/website/landfire). Only percent shrubland and grassland cover were used in the final analysis because forest cover was highly negatively correlated with grassland cover and cover in the “other” category was uncommon.

We included both direct and indirect measures of nutrient availability and soil conditions in our models. We calculated soil pH and percent organic matter from the U.S. General Soil Map STATSGO (http://soildatamart.nrcs.usda.gov). We used several proxies for nitrogen and phosphorous availability, the two minerals generally most limiting to plant productivity. Rock phosphorous and nitrogen at each site were derived from maps of bedrock percent phosphorous and nitrogen composition (J. Olson, Utah State University, unpublished data) based on the Preliminary Integrated Geologic Map Databases for the United States (Ludington et al. 2007). The percent of area with woody nitrogen fixing species was calculated as the proportion of a 200-m buffer around sites where nitrogen fixing plants were listed as occurring in a national vegetation map

(LANDFIRE Map of Biophysical Settings from U.S. Department of the Interior, Geologic Survey, http://gisdata.usgs.net/website/landfire).. Atmospheric nitrogen deposition data were extracted from the US Environmental Protection Agency Atmospheric Modeling and Analysis Division Watershed Deposition Tool (Schwede, Dennis & Bitz 2009). Abbreviations used in subsequent text for all predictor variables are listed in Table 2.1.

Dispersal measure

We calculated dispersal constraint as the squared inverse cumulative distance between a given site and known occupied sites. This measure has been effective in recent work (Allouche et al. 2008). Furthermore, though we use presence and absence data in our study, this measure can also be used with presence-only data (Václavík & Meentemeyer 2009), increasing its potential utility in other applications. The dispersal value D_i at site *i* is the summation of the inverse squared Euclidean distance, d_{ij}, between site *i* and all known occupied sites *j*:

$$D_i = \sum_{j=1}^{N} \frac{1}{(d_{ij})^2}$$

Model methods

We used an ensemble of 4 models, including generalized linear models (GLM), classification trees (CT), Random Forests (RF), and Boosted Trees (BT), to identify environmental factors associated with the distributions of our study species. Each of these methods has performed well in recent comparative studies (Segurado & Araujo 2004; Cutler et al. 2007; Guisan et al. 2007). Ensemble approaches to distribution modeling have been increasingly favored as a way to minimize uncertainties and distinguish between model signal and noise (Araújo & New 2007). Furthermore, because we were interested in comparing model accuracy between species, we did not want to rely on a single model form in case the underlying algorithm of that form fit one species better than the other. For example, simple logistic regression without interactions could model one species better than another if one species had more linear relationships with predictor variables than the other. We optimized model parameters and selected a parsimonious set of predictor variables to create a habitat-only model for each model form before adding the dispersal variable. All analyses were done in R 2.12.1 (R Development Core Team 2010).

GLM are extensions of linear models that allow for both user-specified distributions for model error terms and for link functions to connect the mean response to the predictor variables. We used the logistic model with a binomial error distribution and a logit-link function. We used a combination of forward and backward model selection with the step function in R, as has been done in other distribution modeling studies that were primarily exploratory (Collingham et al. 2000; Dullinger et al. 2009). We considered adding quadratic terms and interactions to models but determined that they added unnecessary complication to model interpretation with marginal benefit to model accuracy. The dispersal model of *C. canadensis* exhibited quasi-separation of the data points. This is different from full separation, when a value of a predictor variable splits the data perfectly into two homogenous groups. With quasi-separation, a predictor variable value splits the data into one homogenous group and the other group remains heterogeneous. Robust parameter estimates cannot be obtained when there is quasi-separation of the data. To account for this, we used the Firth penalized likelihood method (Firth 1993) with the R package logistf (http://CRAN.R-project.org/package=logistf) for the dispersal model of *C. canadensis.*

CT use predictor variable values to partition data into groups that are increasingly homogenous in regards to response variable values. For example, the first split in a tree could create two groups of sites divided by a threshold value of summer precipitation, with mostly presence records in one group and mostly absence records in the other. Trees are grown with a large number of splits and then pruned to an optimal number of splits that balances correct classification and inclusion of interactions with prevention of over-fitting. We used rpart (http://CRAN.R-project.org/package=rpart) to produce classification trees after weighting data to have an equal number of presence and absence sites for each species. We pruned final trees to the modal number of splits that had an error rate within 1 SE of the lowest 10-fold cross-validation misclassification rate across 50 model runs (De'ath & Fabricius 2000). To avoid over-fitting, we created the dispersal model by selecting a new optimal number of splits after adding the dispersal constraint to the variables selected in the final habitat-only model.

RF average results from many un-pruned classification trees to create a more stable and accurate model (Cutler et al. 2007). Each tree is built with a bootstrapped sample of the data, and the variables used for each split are selected from a random subset of the total predictor variables. We used randomForest (http://cran.r-project.org/doc/Rnews/Rnews_2002-3.pdf) with 1000 trees in each model. We used default values for the bootstrapped sample size and number of predictor variables selected at each split. We performed variable reduction to increase model accuracy and eliminate variables that lacked strong predictive power, generally following the methods laid out in Genuer, Poggi, and Tuleau-Malot (2010). Variables were ranked in importance by determining the mean values of the mean decrease in accuracy obtained from 50 model runs. We then ran a series of models from the most complex with 20 variables to a single variable model, each time eliminating from the remaining variables the one with the lowest importance ranking. We calculated two accuracy statistics, the true skill statistic (TSS) and area under the receiver operating characteristic curve (AUC), across 50 runs of each model and selected as the final model the most parsimonious model within 1 SE of the highest accuracy value.

BT is another ensemble method for combining many classification trees into a final model. Each tree is built with iteratively reweighted data, with cases incorrectly classified in the previous tree more heavily weighted in the subsequent tree to improve prediction for harder-to-predict cases. We used package gbm (http://CRAN.R-project.org/package=gbm) in R, setting the number of nodes in each tree to two and the out-of-bag fraction to 0.75 after some initial parameter exploration (Elith, Leathwick & Hastie 2008). We set the learning rate to 0.001 for *P. arundinacea* and 0.003 for *C. canadensis* to ensure that the optimal number of trees in each model was between 3000 and 5000 to balance model stability with decreased processing time. We used gbm.step and gbm.simplify functions developed by Elith, Leathwick and Hastie (2008) for initial parameter exploration and for variable reduction. Gbm.simplify determines error rates for a series of models, with the least important predictor variable dropped in each subsequent model. Mean error rates and standard errors for each model are calculated across the folds of a 10-fold cross-validation. We selected the smallest model within 1 SE of the lowest cross-validation error rate as our final BT model. We selected a new optimal number of trees when we added the dispersal constraint for the final dispersal model.

Model evaluation and comparison

We used 10-fold cross-validation to calculate accuracy statistics for each model (Fielding & Bell 1997) with the final model parameters and predictor variables determined in the initial model-fitting stage. We used mean values obtained over 10 separate cross-validation runs to obtain more stable accuracy metrics. We focused on two accuracy measures for model comparison, TSS and AUC. TSS is the sensitivity (percent of presences correctly predicted) + specificity (percent of absences correctly predicted)-1 of model predictions (Allouche, Tsoar & Kadmon 2006). TSS requires a threshold to convert predicted probabilities to 0s and 1s. We used species observed prevalence in the study area as the threshold of conversion (Freeman & Moisen 2008), except for CT, which had a threshold of 0.5 because these models were created with weighted data. TSS includes information about both false presence and false absence rates in a single measure and is less affected by species prevalence rates than other measures (Allouche, Tsoar & Kadmon 2006). AUC evaluates model accuracy using a plot of sensitivity versus 1 minus specificity at all possible thresholds for converting probabilities to 0s and 1s (Fielding & Bell 1997). As the threshold value increases, a good model will have an increasing number of true positives while maintaining a low false presence rate until the point where almost all presences are correctly modeled. AUC values of 1 indicate perfect fit whereas values near 0.5 perform no better than random.

Variable importance

We qualitatively assessed the uniformity of variable selection across model methods for each species as well as the direction of the relationship between selected variables and species presence. Variables found in the majority of models with consistent relationship directions were considered the most robust. We used the sign of parameter estimates to determine the direction of the relationship in GLM. We interpreted tree splits in CT to determine if the variable relationship was positive or negative. In RF and BT, we examined the general trend in partial dependence plots, which are plots of the marginal effect of a predictor variable when other variables are held constant. We focused our interpretation on the plot area between the first and tenth deciles of data to avoid the influence of outliers. Relationships that were not clearly positive or negative in the partial plots were left unidentified. We used bivariate partial dependence plots to determine whether there were strong interactions in the BT and RF models.

Results

Comparison of model performance

All models performed at acceptable (AUC>0.70) or excellent (AUC>0.80) levels (Hosmer & Lemeshow 2000) except for both CT models of *P. arundinacea* (Table 2.2). The median AUC and TSS values of habitat-only models were higher for *C. canadensis* than for *P. arundinacea* (Fig. 2.2), though GLM performance was marginally better for *P. arundinacea.* Fit improved with the addition of the dispersal variable with the exception of the AUC value for the CT model of *C. canadensis* (Table 2.2). Model fit with the dispersal variable showed more improvement for *P. arundinacea* than for *C. canadensis* (Fig. 2.2).

Relationships of predictor variables to species' presence

Final models without dispersal constraints showed consistency in the selected final predictor variables and the direction of the relationship between predictor variables and the presence of the species of interest (Table 2.3, Figs. A.1-A.4). Most models predicted greater *P. arundinacea* presence at warmer sites with longer growing seasons, higher nutrient levels, and lower stream slopes. There was also evidence suggesting greater presence at sites wetter in summer, drier in winter and closer to roads. *Calamagrostis canadensis* occurred at wet, cool, acidic sites further from roads with higher organic soil content and lower stream slopes. Some models also showed a negative relationship between the presence of *C. canadensis* and grazing, shrub cover, and nutrient levels. The dispersal variable was positively associated with presence for both species (data not shown).

Bivariate partial dependency plots of Pmin with Tmin (Fig. 2.3a) and among Tmin, Tmax, and Gdays (data not shown) showed that the effect of any one of these climatic variable became less noticeable at high values of any of the other variables, indicating, for example, that *either* high Pmin *or* high Tmin was adequate to predict a high probability of *P. arundinacea* presence. In contrast, high Tmax (Fig. 2.3b) or Gdays (data not shown) only moderately increased the probability of presence unless there was also high Pmin. Interactions for *C. canadensis* were not as pronounced as those for *P. arundinacea* and are not reported.

Discussion

Dispersal processes in native versus invasive species

Our study is the first we know of that compares distribution models for native and introduced species to determine the extent to which dispersal processes contribute to model accuracy. Our results support the hypothesis that introduced species are further from equilibrium than native species. Two important insights are highlighted by our results. First, overall improvement in model fit with the dispersal constraint was relatively low. The lack of a stronger effect could mean that habitat-only models are adequate for distribution models of introduced species, particularly in studies like this one that 1) incorporate predictor variables such as road density that may be proxies for dispersal and 2) involve a species that has been introduced to the study area for a relatively long time (in this case, over 100 years). Conversely, the fact that we found a dispersal signal despite the coarseness of our dispersal variable could mean that dispersal processes are more important in affecting distributions than implied by our results. We may have detected a stronger effect if we were able to include data on all occupied sites rather than only the sampled sites or if we were able to include data on wind patterns or landscape features that may affect dispersal. These two possibilities should be explored further through comparisons of models of recently and historically introduced species and comparisons of the effectiveness of different methods of quantifying dispersal potential. The second insight from our study is that incorporation of dispersal constraints can improve model results for both native *and* introduced species. Our native study species, *C. canadensis*, improved almost as much as our invasive study species, *P. arundinacea*, with the addition of the dispersal constraint. Several recent studies suggest that plant species may in general be more limited by environmental rather than dispersal factors (Araújo & Pearson 2005; Moore & Elmendorf, 2006). However, the relative degree to which these factors control distributions probably varies among species (Leathwick 2009), suggesting that some native and invasive species may show greater improvement than that seen in this study.

The dispersal variable we used in our study is only a coarse measure of site propagule pressure. We do not have data on all potentially occupied sites in our study area. Instead, we used an estimate of relative regional propagule pressure by taking a summation of the weighted distance to known sources. We believe this measure is an adequate approximation of regional propagule pressure because our data is from randomly selected sites across a large region. We also assume that dispersal for our study species occurs primarily as a function of the Euclidean distance between sites instead of taking into account the roles of waterways and landscape barriers in affecting dispersal. This assumption is supported by research that shows that gene flow for riparian plant species does not occur in a unidirectional (i.e. downstream) manner (Honnay et al. 2010). Furthermore, seeds of our study species are probably predominantly wind rather than water dispersed. Seed dispersal by wind is likely a function of Euclidean distance from source as well as additional landscape and wind pattern factors not considered in this study. Development of less coarse methods for modeling dispersal processes in regional-scale distribution models may lead to greater predictive ability and more robust estimates of site vulnerability to invasion.

Differences in model accuracy between species can potentially be caused by factors other than lack of equilibrium. Species with small range sizes or narrow environmental requirements are modeled more accurately than generalist species (Segurado & Araujo 2004; Elith et al. 2006; Guisan et al. 2007). We selected study species with similar North American distributions and growth requirements (http://plants.usda.gov/) to help account for this potential issue. Species could also be differentially affected by ecological processes missing from models, such as biotic interactions or unmeasured environmental factors (Fielding & Bell 1997). We cannot rule out the possibility that we did not include a predictor variable important to one, but not the other, species. However, our use of two strongly competitive species (Wetzel & Valk 1998; Hangs, Knight & Van Rees 2002) and use of a wide variety of predictor variables lowered the risk of excluding environmental factors important to one or both species. The fact that the dispersal constraint improved model fit for the invasive species more than for the native suggests that initial model differences may in fact be due to differences in the degree to which these two species are at equilibrium.

Factors related to P. arundinacea invasion

Our results revealed several previously unreported relationships between *P. arundinacea* and site characteristics that have important implications for the future distribution of this species. Though *P. arundinacea* is reportedly adapted to cool, moist areas (Lavergne & Molofsky 2004), we found that this species is more common in warmer areas with adequate summer rainfall within our study area. *Phalaris arundinacea* also appears to be cold-limited, though these results may be strain-specific. A study near Anchorage, Alaska found that some source populations of *P. arundinacea* were extremely winter-tolerant, although the majority of populations exhibited low to no winter survival (Klebesadel & Dofing 1991). The phenotypic variability found in that and other studies (Sahramaa & Jauhiainen 2003; Lavergne & Molofsky 2007) suggests that the climatic relationship we observed cannot necessarily be extrapolated to populations beyond our study area where different strains of the species may have been introduced. Climate change could potentially have a positive, negative or neutral effect on our study species because our study area is predicted to see both increased temperatures and decreased summer precipitation (Karl, Melillo & Peterson 2009).

Another important management implication of our study is that any increase in nitrogen availability, including from natural sources, may make sites more susceptible to *P. arundinacea* invasion*.* Experimental research has shown that the growth and competitive ability of *P. arundinacea* increases with increased levels of available soil nitrogen (Wetzel & Valk 1998; Green & Galatowitsch 2002; Kercher & Zedler 2004). These studies have generally been undertaken to address the effect of agricultural runoff on wetland invasion. Our study shows that even in areas removed from agricultural runoff, other sources of nitrogen can increase invasion success. *Phalaris arundinacea* was more common at sites with higher nitrogen deposition, even though deposition levels were at the lower end of the range of levels expected to affect some ecosystems in the western United States (Fenn et al. 2003). The presence of native communities of nitrogen fixers may also increase the risk of *P. arundinacea* invasion. Careful species selection, including use of native species with low nitrogen content and avoidance of nitrogen-fixers, may be vital for riparian restoration projects that seek to limit *P. arundinacea* invasion.

The degree to which *P. arundinacea* requires disturbance for invasion is unknown. Restored and natural wetlands in Wisconsin and Oregon have similar levels (cover and percent of wetlands occupied, respectively) of *P. arundinacea* invasion (Ashworth, 1997; Magee et al. 1999), suggesting that disturbance may not be required in those systems. Ringold, Magee and Peck (2008) found that *P. arundinacea* was more common near disturbances in western riparian areas. This latter study included sites with more urban and agricultural influence than sites in our study area. Our results suggest that some disturbance may be important for invasion. Roads may be associated with *P. arundinacea* invasion because vehicles on roadways spread seed or because roads are indicators of other disturbances near sites, such as construction or logging (Parendes & Jones 2000). Sites disturbed by livestock grazing, on the other hand, had a lower likelihood of containing *P. arundinacea*, similar to findings in riparian areas in Wisconsin (Paine & Ribic 2002). These results contrast with experimental grazing manipulations that suggest that grazing either has no impact (Hillhouse, Tunnell & Stubbendieck 2010) or actually increases the biomass of *P. arundinacea* (Kercher & Zedler 2004). The relationship between *P. arundinacea* and livestock grazing merits further evaluation.

Conclusions and recommendations

Our study supports the idea that introduced species are less likely to meet the distribution modeling assumption of equilibrium than native species. Although the effect for our study species was not large, species more recently introduced or more dispersal-limited may benefit greatly from incorporating dispersal processes into models. The use of dispersal variables should be evaluated further to determine situations where they provide the greatest benefit for models of both introduced and native species. Furthermore, a broader suite of dispersal indices should be tested. Development of more refined dispersal variables should lead to greater model improvement and thus more management utility. We also recommend the use of predictor variables that relate directly to dispersal processes, such as road density and grazing pressure, because interpretation of models with these variables has the potential to provide direct management recommendations.

The fact that distribution models are correlative and not mechanistic can limit the inference we can draw from them and make it difficult to extrapolate results to new areas. Nonetheless, relationships found in models can be useful for providing management guidelines in the absence of other data and for suggesting areas for future research. Within our study area, monitoring for *P. arundinacea* should be focused on areas near roads and with higher nitrogen levels. Managers should also anticipate the potential for increased invasion with climate change induced temperature increases, though this may be modulated by decreased summer precipitation. We also recommend research on strain-specific climatic tolerances and the distribution of strains across the United States in order to better understand how climate change will affect this species.

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Table 2.1. Predictor variables used in species distribution models. Range and measurement units listed for continuous variables.

Variable	Description	Range	Units
Continuous variables			
Pmin	mean monthly precipitation of the driest month of the year	7-96	mm
Pmax	mean monthly precipitation of the wettest month of the year	28-273	mm
Tmin	mean monthly temperature of the coldest month of the year	-18.8--3.1	°C
Tmax	mean monthly temperature of the hottest month of the year	15.5-31.9	°C
Gdays	mean number of annual growing days (days between first and last freeze)	10-176	days
Grazing1k	percent of 1-km buffer around site with grazing allotments	0-100	%
Rd1k	length of roads in 1-km buffer around site	0-30408	m
RdNear	distance from site to nearest road	0.3-19220	m
RockP	percent phosphorous in the underlying bedrock at sites	0.07-3.1	%
RockN	percent nitrogen in the underlying bedrock at sites	0-0.07	%
Nfixer	cover of woody nitrogen fixing species at site	0-100	%
Ndep	atmospheric nitrogen deposition	1-5.3	kg/ha
OM	percent of fines composed of organic matter	1.2-10.8	%
pH	pH of site	5.1-8.5	
Shrub	cover of shrubland at sites	0-92	%
Grass	cover of grassland at sites	0-100	%
Slope	slope of site stream segment	0-25.5	%
Baseflow	stream flow attributed to ground-water discharge into streams	31-89	%
Categorical variables			
Fire	presence/absence of fire within last 10 years at site		
GrazingSite	presence/absence of grazing allotments at site		

Table 2.2. Accuracy measures and number of variables in final models of *Calamagrostis canadensis* and *Phalaris arundinacea* presence. Model methods include generalized linear models (GLM), classifications trees (CT), Boosted Trees (BT), and Random Forests (RF). Habitat-only models include an optimized subset of predictor variables whereas dispersal models incorporate dispersal constraints into the habitat-only model. See Methods for a description of AUC and TSS, the accuracy metrics used.

		Calamagrostis canadensis			*Phalaris arundinacea*		
	Model method	# variables	AUC	TSS	# variables	AUC	TSS
Habitat-only models	GLM	10	0.779	0.411	11	0.781	0.425
	CT	6	0.740	0.400	1	0.647	0.372
	BT	9	0.811	0.479	7	0.769	0.382
	RF	14	0.819	0.503	12	0.771	0.396
Dispersal models	GLM	11	0.787	0.428	12	0.792	0.449
	CT	1	0.704	0.427	2	0.686	0.373
	BT	10	0.820	0.484	8	0.785	0.408
	RF	15	0.830	0.516	13	0.800	0.442

Table 2.3. Direction of relationships between species presence and predictor variables. Model methods include generalized linear models (GLM), classifications trees (CT), Boosted Trees (BT), and Random Forests (RF). + indicates positive, - indicates negative and ? indicates unclear relationship with presence.

	Species and Model Method							
	Calamagrostis canadensis				*Phalaris arundinacea*			
	CT	GLM	RF	BT	CT	GLM	RF	BT
Pmin	+	+	+	+		+	?	+
Pmax			+	+		-	-	
Tmin		-	-	-	+	+	+	+
Tmax			-			+	+	+
Gdays	-	-	-	-		+	+	+
GrazingSite						-		
Grazing1k		-	-				-	
Rd1k			?				+	
RdNear		+	+	+		-	-	
Fire		+						
RockP			-	-			+	
RockN								
Nfixer						+		+
Ndep	+		-			+	+	+
OM	+	+	+	+				
pH		-	-	-			?	
Grass								
Shrub		-				-		
Slope	-	-	-	-		-	-	-
Baseflow			+					

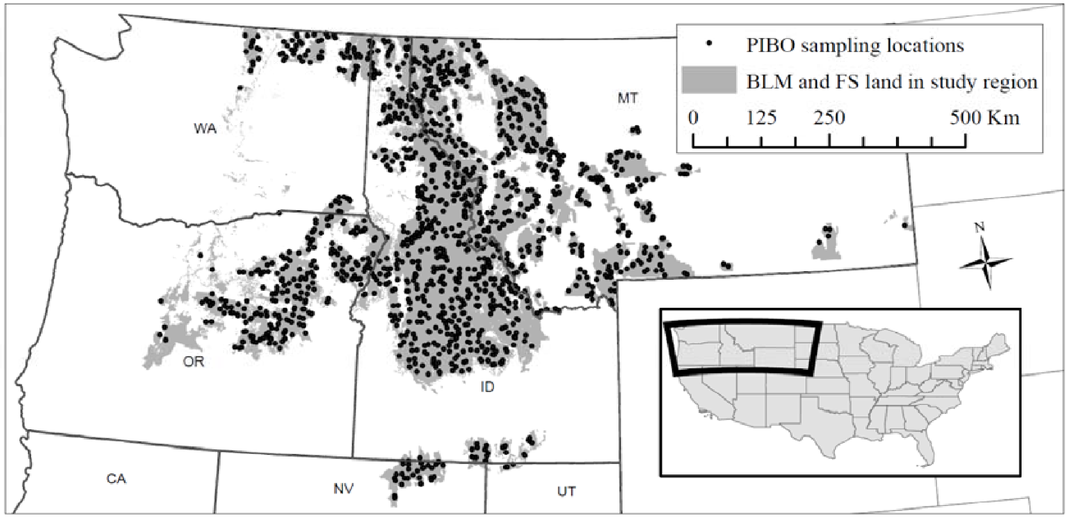

Figure 2.1. Study area and sampling locations for the USFS PIBO Effectiveness Monitoring Program. All sites are located on federally owned Bureau of Land Management and Forest Service land.

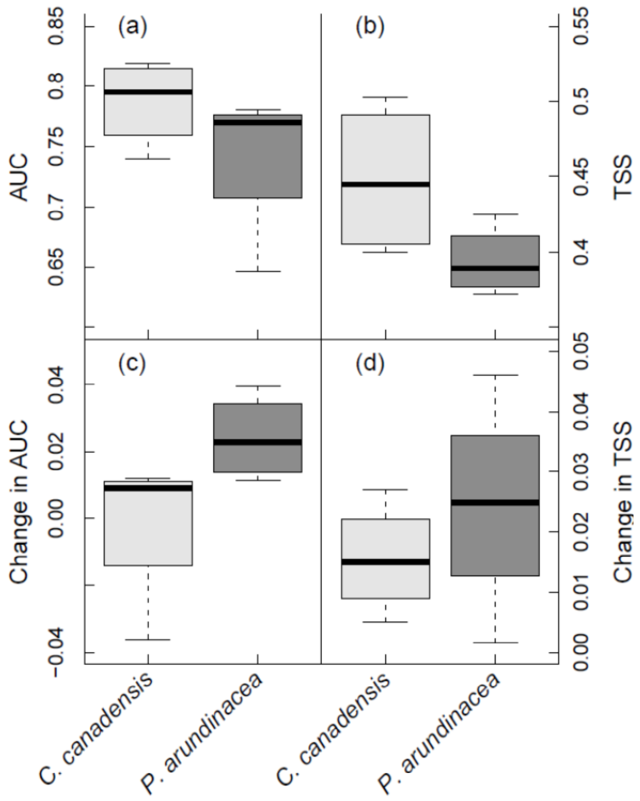

Figure 2.2. Comparison of model accuracy for habitat-only models (a, b) and change in model accuracy with the addition of dispersal constraints (c, d) for models of the distributions of the native *Calamagrostis canadensis* and the invasive *Phalaris arundinacea***.** Accuracy measures compared include AUC and TSS; see Methods for explanations. Boxplots show accuracy measures across four model forms, with boundaries of boxes indicating the first and third quartiles, solid lines marking the medians and whiskers indicating data beyond 1.5 times the interquartile range.

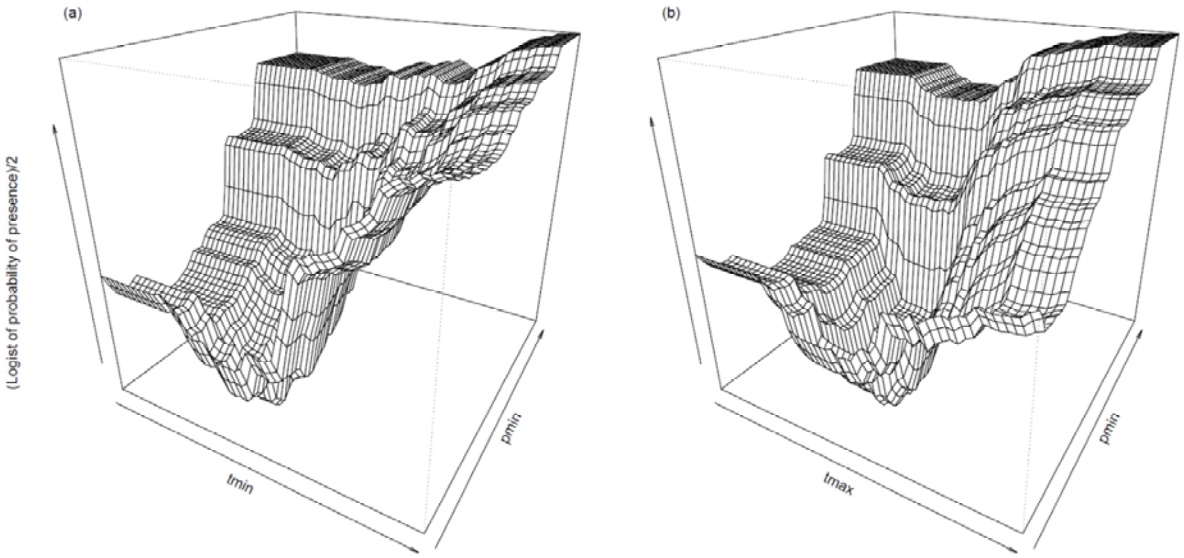

Figure 2.3. Bivariate partial dependence plot of Pmin and Tmin (a) and Pmin and Tmax (b) in the final Random Forest model of *Phalaris arundinacea* presence. See Table 2.1 for variable description.

CHAPTER 3

CLIMATE CONDITIONS AND RESOURCE AVAILABILITY DRIVE INVASIVE PLANT ESTABLISHMENT IN RIPARIAN AREAS IN THE COLUMBIA AND MISSOURI RIVER BASINS

Abstract

1. Understanding the natural and anthropogenic characteristics that make sites more susceptible to invasion can inform monitoring and control efforts and help determine appropriate management actions to lower invasion risk. Research on site invasibility has frequently either focused on individual species or on overall levels of sites invasion by looking at abundance or richness of invaders.

2. In contrast, we simultaneously looked for region-wide patterns of site invasibility and species-specific habitat relationships. We modeled the distributions of 11 invasive plant species along riparian areas in the northwestern United States using Random Forests. Variables related to climate, disturbance, nutrient and soil conditions, land cover, and site hydrology were included in the models.

3. We found that climate, soil, and nutrient variables were more important for predicting the distribution of invasive plant species than land cover or factors related to disturbance. We also found that there was a general pattern related to invasion for almost all species, with invasion more likely to occur at hot dry sites near roads with high grass or shrub cover and high nutrient levels along streams with lower baseflow values.

5. *Synthesis and application.* We recommend nutrient management, monitoring and control measures along roadways, and long-range planning for climate change as three

important management actions in our study area. Our approach should be applied to additional regions to see if discrete patterns of invasibility emerge in other areas. Examining patterns across a broad range of regions could help suggest general mechanisms of invasion as well as provide region-specific management recommendations.

Introduction

Non-native plant species become invasive when they can both establish self-sustaining populations and spread across the landscape to new sites (Richardson et al. 2000; Theoharides & Dukes 2007). Anthropogenic disturbances such as changing fire regimes (Keeley 2006; Vicente et al. 2010), increased grazing pressure (Kercher & Zedler 2004; Diez et al. 2009), and nutrient addition from agricultural runoff or atmospheric nitrogen deposition (Bakker & Berendse 1999; Brooks 2003) can increase the establishment success of invaders. Variability in background nutrient levels (Maron & Jefferies 1999; Prieur-Richard et al. 2002), natural disturbance regimes (Stohlgren et al. 1998; Hood & Naiman 2000), and other ecosystem characteristics can also influence site susceptibility to invasion. Site attributes may also determine how easily invasive species spread. Dispersal of invasive species may be higher in areas near roads (Parendes & Jones 2000; Hansen & Clevenger 2005) or at sites that have novel grazing pressure (Hobbs & Huenneke 1992; Bartuszevige & Endress 2008).

Understanding both the anthropogenic and natural site traits that increase site susceptibly to invasion can inform monitoring and management decisions. Sites with traits that increase risk of invasion can be targeted for early detection and rapid response programs (Pyšek & Richardson 2010). Furthermore, managing site attributes related to invasion may be more effective than managing individual species if site conditions are such that reinvasion with a variety of species is likely to occur following control efforts (Hobbs & Humphries 1995). For instance, if invasion occurs at sites with high nitrogen levels, restoration projects can use soil amendments or plant bridge species to lower invasion risk (Vasquez, Sheley & Svejcar 2008). Also, identifying region-specific relationships between grazing and site invasibility may be helpful since studies have found that livestock grazing has both positive and negative effects on invasion risk, depending on the study and region (Alpert, Bone & Holzapfel 2000). An understanding of site traits associated with invasion may be particularly important in the face of climate change as areas previously perceived as resistant to invasion may become more vulnerable (Pauchard et al. 2009).

Empirical work looking at site characteristics associated with invasion has generally looked at associations for one or a few invasive species (Evangelista et al. 2008; Ibáñez et al. 2009b; Loo et al. 2009), looked at one or a few factors related to invasion (Wilson et al. 1992; Matthews et al. 2009), or modeled richness and/or abundance of all exotic species as a function of site attributes (Ohlemüller, Walker & Wilson; Ibáñez et al. 2009a; Catford et al. 2011). However, studies of the abundance of exotic species provide information about dominance of invaders, not initial establishment and regional spread. In contrast to other work, in this study we simultaneously looked for region-wide patterns of site susceptibility and species-specific habitat relationships. We wanted to understand both the types of factors most important for predicting where invasion occurs and whether drivers of invasion were similar across a group of invasive species. Our research addressed two primary questions: (1) What types of variables (e.g.

climatic, nutrient-related, disturbance) are important for predicting the distribution of invasive plant species? and (2) Are there specific factors that make sites susceptible to invasion by a range of species or is invasion susceptibility species-specific? We modeled species distributions for 11 invasive species in riparian areas in the northwestern United States with predictor variables related to climate, disturbance, nutrient and soil conditions, land cover, and site hydrology. We used model results to provide a better understanding of what makes some sites more prone to invasion and to provide management advice for our study region.

Methods

Study area and species data

The data we used to build our models was collected by the U.S. Forest Service's (FS) PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program (PIBO) (Henderson et al. 2005). PIBO collects data on randomly selected stream segments on federally owned lands in the eastern Columbia and western Missouri River Basins, a region that includes parts of eastern Oregon and Washington, northern Utah and Nevada, and much of Idaho and Montana (Fig. 3.1). These stream segments range in length from 80 to 500 m, with a mean of 191 m. Vegetation data at each site are collected in 20-cm x 50-cm Daubenmire quadrats placed along the greenline, the first location with at least 25% perennial vegetation cover, and in cross-sectional transects that extend 9.5 meters from the stream edge. Only sites with at least 27 cross-sectional and 40 greenline quadrats were included in the analysis. A species was considered present at a site if it was found in at least one quadrat during at least one survey. There were a total of 1138 sites in the Columbia River Basin and 191 sites in the Missouri River Basin included in this analysis.

Study species

We focused our study on all plant species listed as noxious weeds in at least one of the states in our study area (http://plants.usda.gov) except for those species occurring at <15 sites. We excluded these low occurrence species because of concerns that there was too little data to effectively model their distributions. State noxious weeds are non-native species that, due to their perceived economic, ecological, and/or socio-political importance, are regulated by law and prioritized for prevention and control programs (Skinner, Smith & Rice 2000). *Bromus tectorum* L. (cheatgrass), though not listed as a noxious weed, was also included in the study because it is a species of particular management concern in the study region. Our final species list included one annual grasses, two perennial grasses, and eight perennial or biennial forbs (Table 3.1).

Predictor variables

We selected predictor variables based both on factors expected to influence the spread and establishment of invasive species and on the availability of data across the study area. We reduced our exploratory set of predictor variables to a set of 20 with Pearson correlations <|0.70|. Data was extracted in ArcMap 10 and Geospatial Modelling Environment 0.5.2 (www.spatialecology.com/gme). Climatic variables were extracted from PRISM data (Daly et al. 2008) and chosen to represent the extremes of conditions that species have to tolerate, including mean precipitation of the driest month, mean precipitation of the wettest month, mean temperature of the coldest month, mean temperature of the warmest month, and mean number of days per year between the first and last freeze.

Road, grazing, and fire history data were used as indicators of site disturbance. Distance to the nearest road and density of roads in a 1-km buffer around each site were calculated using road data from TIGER (U.S. Census Bureau 2009) and from unpublished FS and Bureau of Land Management (BLM) spatial data. The least conservative road value was used at each site since readily available road data is often under-representative of true road density (Hawbaker & Radeloff 2004) and this trend was observed in a random sample of sites examined in Google Earth. Grazing information was obtained from FS and BLM spatial data based on the location of grazing allotments. We included both a categorical variable for grazing presence or absence at sites as well as the percent of a 1-km buffer around sites with grazing allotments. Fire data was extracted from Monitoring Trends in Burn Severity (Eidenshink et al. 2007). Sites were considered recently burned if they experienced a fire anytime between 1993 and 2008.

We looked at two measures of hydraulic conditions at sites. The slope of the site stream segment was calculated using 30-m digital elevation models (Gesch et al. 2009). Slope is a strong predictor of unit stream power, which is indicative of flooding force (Bendix 1997). Baseflow values were extracted from the USGS Base-flow Index Grid for the Conterminous United States (Wolock 2003). Baseflow is the percentage of total stream flow that comes from ground water discharge as opposed to rainfall events and is often used as an indicator of low-flow conditions (Smakhtin 2001). Large baseflow values indicate little fluctuation in stream water levels and little responsiveness to large rain events, while low baseflow values indicate large water level fluctuations and more contribution of seasonal rain events to stream flow.

The percent of each site with grass, shrub, and tree cover as the dominant over-story vegetation was calculated from a national vegetation map (LANDFIRE National Existing Vegetation Type layer from U.S. Department of the Interior, Geologic Survey, http://gisdata.usgs.net/website/landfire). Development and agriculture were not included in our analysis because these land cover types were absent at sites and relatively rare in the vicinity of sites. Only grassland and shrubland cover were used in the final analysis because forest and grassland cover were highly correlated (Pearson correlations <-0.9).

We used a variety of data to provide both direct and indirect measures of nutrient availability and soil conditions at sites. We extracted pH and percent soil organic matter from the U.S. General Soil Map STATSGO2 (http://soildatamart.nrcs.usda.gov). Rock phosphorous and nitrogen at each site were derived from maps of bedrock percent phosphorous and nitrogen composition (J. Olson, Utah State University, unpublished data) based on the Preliminary Integrated Geologic Map Databases for the United States (Ludington et al. 2007). The total cover of nitrogen fixing species at each site was calculated from PIBO vegetation data. All species in the Fabaceae family and species in the genera *Alnus*, *Ceanothus*, and *Elaeagnus* were considered nitrogen fixers. Atmospheric nitrogen deposition data were extracted from the US Environmental Protection Agency Atmospheric Modeling and Analysis Division Watershed Deposition Tool (Schwede, Dennis & Bitz 2009). Abbreviations used in subsequent text for all predictor variables are listed in Table 3.2.

Modeling methods and variable assessment

We created distribution models for each species using Random Forests with the randomForest package in R 2.12.1 (Liaw & Wiener 2002; R Development Core Team, 2010). This model form has performed well for distribution modeling in recent work (Cutler et al. 2007; Thomaes, Kervyn & Maes 2008) and automatically includes interactions between variables in models. Random Forests averages results from many un-pruned classification trees to create models that are more stable and accurate than single classification trees (Cutler et al. 2007). Each tree is built with a bootstrapped sample of the data, and the variables used at each split are selected from a random subset of the total predictor variables. We used 1000 trees in each model and the default package values for the bootstrapped sample size and number of predictor variables selected from each split. Random Forests calculates the mean decrease in accuracy for each variable as the normalized difference in classification accuracy between models with the original values for the variable of interest and models where that variable is randomly permuted. Higher values indicate that a variable contributes more towards classification accuracy. We obtained variable importance values by averaging the mean decrease in accuracy for each variable and species combination across ten model runs. For every species, we divided each predictor variable’s importance value by that species’ highest variable importance value. This provided us with a scaled variable importance index, where the most important variable has a value of 1.00 and a variable with an index value of 0.50 has half the importance of the top variable. We used this variable importance index to compare the contribution of predictor variables among species. We used partial dependence plots to determine the relationship between variables and presence of each species, focusing in particular on the area between the first and tenth deciles of data to avoid relationships strongly influenced by outliers. These plots show the marginal effect of a predictor variable when other variables are held constant. Relationships were identified as positive, negative, or flat, or left unidentified if unclear.

We obtained accuracy measures for distribution models using 10-fold cross validation (Fielding & Bell 1997), taking the average across ten runs to obtain more stable results. We report percent correctly classified (PCC), sensitivity, specificity, and area under the receiver operating characteristic curve (AUC). The first three measures require that predicted probabilities of occurrence are converted to 0s and 1s. We used species' observed prevalence in the study area as the threshold for conversion (Freeman & Moisen 2008). PCC is the percent of all sites where the model prediction is correct. Sensitivity is the percent of presences correctly classified and specificity is the percent of absences correctly classified. AUC is the area under the curve of a plot of the sensitivity versus 1 minus the specificity at all possible thresholds. As the threshold value increases, a good model will have an increasing number of true positives while maintaining a low false presence rate until the point where almost all presences are correctly modeled. An AUC value of 1 indicates perfect model fit and 0.5 indicates no better than random.

Results

Model evaluation

All models performed at acceptable (AUC >0.7) or excellent (AUC>0.8) levels (Hosmer & Lemeshow 2000), except for the model of *C. arvense* which had an AUC of 0.662 (Table 3.3). PCC values ranged from 58.6% for *C. arvense* to 76.1% for *H. perforatum*, with a mean of 68%. Sensitivity, with a mean of 72.6%, was higher than specificity, with a mean of 67.6%, for all species except *E. repens*, meaning that models generally were better at predicting presence than absence.

Variables important for predicting species' distributions

Variables related to climate were the two most important model variables for all species (Table 3.4). Precipitation and temperature variables generally had higher importance values than Gdays and had the four highest median variable importance indices of all variables (Fig. 3.2). Variables related to soil and nutrient conditions ranked as the next highest contributors to model performance, though the importance of these variables varied more among species and by the specific variable. The top variable in each of the remaining categories–disturbance, land cover, and hydrology–had similar median variable importance indices to one another. Variables in these categories showed considerable heterogeneity in importance indices between species. For example, Grass (land cover variable) had a variable importance index of 0.81 for *B. tectorum* and 0.29 for *H. perforatum* (Table 3.4). Most species had at least one disturbance variable with relative importance at least half that of their most important model variable, except for *R. acris* and *H. perforatum*, where all disturbance variable importance values were less than 0.44. Fire was considerably more important for three species–*B. tectorum, C. vulgare and E. repens*–than for all the other species, where this variable made close to no contribution to model performance.

Factors related to site susceptibility

Over 60% of the species had a positive relationship with Gdays, Tmin, and Tmax and a negative relationship with Pmin and Pmax (Table 3.4, Figs. B.1-B.11). *P.*

arundinacea, T. vulgare, and *H. perforatum* were the only species that showed a positive relationship with Pmin and/or Pmax. Noxious weeds were also consistently associated with higher nutrient levels. All species had a positive relationship with Nfixer and RockN and most with RockP and Ndep. OM and pH did not have consistent patterns across species. Grass and Shrub had a positive relationship with presence for all species except *H. perforatum*, which showed a flat relationship. Six of the 11 species had a negative relationship with Baseflow, though many species also had an unclear relationship with this variable. Nine of 11 species had positive relationships with Fire and Rd1k and negative relationships with RdNear. One species, *H. perforatum*, was more likely to be present in areas with fewer roads. There were about the same number of species with a positive association with grazing as those with a negative association, with several species showing no relationship.

Discussion

Variables important for predicting species' distributions

Abiotic environmental factors related to climate and soil and nutrient conditions were more important for predicting the distribution of invasive plant species than land cover or factors related to disturbance. This fits with several recent frameworks that discuss invasion as a series of stages with filters determining progress from one stage to the next and climate and/or abiotic conditions serving as the first filters after a species is initially introduced to a broad region (Richardson et al. 2000; Richardson & Pyšek 2006; Theoharides & Dukes 2007; Milbau et al. 2009). In contrast to what we found, Catford et al. (2011) found that whether or not a site had *at least one* exotic species was more strongly predicted by disturbance and biotic factors than it was by climatic variables. The difference in results may indicate that disturbance and biotic factors have a more consistent relationship with invasion success while tolerance to climatic factors varies more between species. Though abiotic drivers were the initial filters, disturbance still had a relatively important role in the distribution of almost all species. The influence of disturbance did not appear to differ between species introduced over 300 years ago (e.g. *T. vulgare*) and species of more recent origin (e.g. *C. biebersteinii)* (see Table 3.1). Disturbance itself and not just its role as an indicator of propagule pressure may be playing a role in creating opportunities for species establishment.

Factors related to site susceptibility

Our study is distinctive because it addresses a wide range of factors simultaneously and individually for a suite of species, revealing a region-wide pattern. Invasion was more likely at hot dry sites near roads with high grass or shrub cover and high nutrient levels along streams with lower baseflow values. This corroborates other studies that have found that warm, dry environments (Wilson et al. 1992; Pyšek, Jarošík & Kucera 2002; Sobrino et al. 2002; Ohlemüller, Walker & Wilson 2006), sparsely or unforested areas (Allen & Shea 2006), high nutrient sites (Jefferies & Maron 1997; Bakker & Berendse 1999; Alpert, Bone & Holzapfel 2000; Brooks 2003; Colautti, Grigorovich & MacIsaac 2006; Loo et al. 2009), and areas near roads (Parendes & Jones 2000; Gelbard & Harrison 2003; Hansen & Clevenger 2005) are more heavily invaded. This also agrees with a meta-analysis that found that anthropogenic activity, disturbance, and resource availability were all positively related to the establishment and spread of non-native species (Colautti, Grigorovich & MacIsaac 2006). An approach undertaken in southeastern Australia modeling the presence or absence of *at least one* non-native species at sites also found more invasion in areas drier and hotter in summer, closer to roads, and with higher soil fertility (Catford et al. 2011).

Roads may promote invasion both by increasing dispersal opportunities and providing conditions that aid establishment. Road traffic can transport seeds and other propagules to new sites (Lonsdale & Lane 1994) and roadsides frequently have suitable conditions for species' establishment, such as low competition and high light levels (Coffin 2007). The roadside pool of invaders can serve as a reservoir for species to move into adjacent areas when conditions are favorable. Roads may also be indicators of other disturbances near sites, such as construction, logging, or higher rates of foot traffic (Parendes & Jones 2000).

We propose two potential explanations for why we found a suite of traits (high nutrients, low baseflow, low precipitation, high temperatures) associated with invasion for most of our study species. First, these traits may relate to processes that make sites more invasible. Community ecology theory points to the importance of resource opportunities for the establishment of new species, including invasive species (Shea & Chesson 2002). High nutrient levels combined with pulsing stream flow and rare rain events in our study area may periodically free up resources to create opportunities for establishment, as predicted by the fluctuating resource hypothesis (Davis, Grime & Thompson 2000). Alternatively, species adapted to these conditions may have been more frequently introduced to the region and thus it would be more likely that some would become invasive (propagule pressure, *sensu* Colautti, Grigorovich & MacIsaac 2006). The majority of our study species were introduced as seed contaminant in crops or forage and therefore may be adapted to a similar suite of conditions. *H. perforatum* and *L.*

vulgare, both introduced as garden ornamentals rather than seed contaminants, showed the most anomalous relationships with the predictor variables. We recommend applying our multi-species modeling approach in other study areas to look more broadly for generalities and to help determine whether these traits are actually related to resource availability or to propagule bias.

While there was a general set of traits that made sites more susceptible to invasion, there was also important heterogeneity between species. The response to livestock grazing was almost equally divided between species more and less likely to be found near grazing allotments. This corroborates a recent review that found no consistent direction of relationship between richness of non-native species and grazing (Díaz et al. 2007). Our results suggest that the effect of grazing on invasive species establishment and spread may be species-specific rather than region-specific. Responses of individual species may be mediated by each species' evolutionary history with grazing (Milchunas, Sala & Lauenroth 1988) or by particular traits that confer resistance (Díaz, Noy-Meir & Cabido 2001).

Management implications and conclusions

Three important region-wide management needs are evident from our study: nutrient management, monitoring and prevention measures along roadways, and long-range planning for climate change. Our research suggests that nutrient management is important both at sites with increased anthropogenic sources of nutrient availability as well as at sites with higher natural background levels of nutrients. Nitrogen control such as planting bridge species that have low nitrogen content can be implemented after fires, heavy flood events, or other disturbances, or as part of restoration projects to reduce invasion potential at sites (Vasquez, Sheley & Svejcar 2008; Perry et al. 2010). Monitoring and subsequent control efforts on roads can not only lower site risk of invasion, but also decrease potential for long-distance spread. Roadside invasive plant surveys can be more cost-effective than randomly placed surveys (Shuster et al. 2005), especially if combined with interior searches when target species are found (Abella et al. 2009). Careful restoration of decommissioned roads (Grant et al. 2010) is important because even roads abandoned for over 20 years show heightened numbers of invaders (Parendes & Jones 2000). Roadless areas can also serve as important strongholds of native plant species (Gelbard & Harrison 2003). Risk of seed transport along roadways can be lowered by implementing wash stations, especially for vehicles at high risk for carrying seed (Bocking, Galway & Brooks 2008).

Unfortunately, climate change is not directly manageable and may provide novel challenges to land managers. Our study region is predicted to see temperature increases between 2 and 5°C by the end of the century, with increased winter precipitation, decreased summer precipitation, and more frequent extreme climatic events such as droughts, heavy rains, and heat waves (Karl, Melillo & Peterson 2009). Warmer temperatures and drier summers may favor many of our study species, making previously unsuitable sites more inhabitable. Furthermore, invasive species may be more adapted for rapid range shifts than native species due to favorable dispersal properties and close association with roads that could help transport them to suitable climates (Dukes & Mooney 1999). Managers can prepare for shifts in invasive species distributions by monitoring sites previously unsuitable to invasion and by surveying and treating invasive species along roadways, which may be the first means by which an invasive species will reach new areas. Some control strategies could become less effective under changing climates, such as if there is a difference between how well biocontrol agents and the invasive species they target can adapt to novel climatic conditions (Hellmann et al. 2008).

Species-specific management strategies should be used to complement our recommendations in areas prone to particular species. While almost all species exhibited a positive relationship with fire, this variable was only important for *B. tectorum, C. vulgare,* and *E. repens.* Sites vulnerable to these species should be monitored after burns so early control efforts can be implemented. Three species are most likely to be found at grazed areas: *C. vulgare*, *C. officinale,* and *L. vulgare*. Grazing regimes at sites with these species may need to be modified in order to control these species. Last, the distributions of *H. perforatum* and *R. acris* were least influenced by distribution factors. For these species, modification of anthropogenic activity may be less important than direct species control.

Our study informs invasion theory by validating the concept of filters acting at different stages of invasion. Furthermore, we identified traits that make sites more vulnerable to establishment by a wide range of species considered noxious weeds. Based on these traits, we determined that nutrient management, road monitoring, and climate change preparation were important management actions for our study region. Our approach should be applied to additional regions to see if discrete patterns of invasibility emerge in other areas. Examining patterns across a broad range of regions could help suggest general mechanisms of invasion as well as provide region-specific management recommendations.

References

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Table 3.1. List of species used in this study along with species code, growth form, date of introduction to the United States and western United States, means of introduction, and methods of reproduction. All information from USDA Forest Service Fire Effects Information database, http://www.fs.fed.us/database/feis/plants/index.html, unless otherwise noted.

Species	Code	Growth Form	U.S. (Western) Introduction Date	Means of Introduction	Methods of Reproduction
Bromus tectorum	BRTE	annual grass	mid-1800s	contaminated crop seed, ship ballast	seed only
Centaurea biebersteinii	CEBI	biennial/perennial forb	late 1800s (post-1920)	contaminated crop seed, ship ballast	primarily seeds, some lateral shoots
Cirsium arvense	CIAR	perennial forb	1600s	contaminated crop seed, ship ballast	seed and lateral roots
Cirsium vulgare	CIVU	biennial forb	1700s (late 1800s)	contaminated crop seed	seed only
Cynoglossum officinale	CYOF	biennial forb	mid-1800s	contaminated crop seed	seed only
Elymus repens	ELRE	perennial grass	1600s[1]	contaminated crop seed [5]	primarily rhizomes, some seed
Hypericum perforatum	HYPE	perennial forb	late 1700s (early 1900s)	intentional for garden cultivation	seed and lateral roots
Leucanthemum vulgare[2]	LEVU	perennial forb	(late 1800s)	contaminated crop seed, intentional for garden cultivation	seeds and rhizomes
Phalaris arundinacea	PHAR	perennial grass	1850[3]	intentional for forage, wastewater treatment, bioenergy crop[3]	seeds and rhizomes
Ranunculus acris	RAAC	perennial forb			seeds and rhizomes
Tanacetum vulgare	TAVU	perennial forb	1600s (late 1800s)	intentional for garden cultivation	seeds and rhizomes

[1] http://www.invasivespeciesinfo.gov/plants

[2] all information for this species from http://www.nwcb.wa.gov/weed_info/Written_findings/Leucanthemum_vulgare.html

[3] Lavergne and Molofsky (2004)

[4] http://www.mt.nrcs.usda.gov/technical/ecs/invasive/technotes/InvasiveTN_27/index.html

[5] http://na.fs.fed.us/fhp/invasive_plants/weeds/quackgrass.pdf

Table 3.2. Variables used in species distribution models with range and units. Categorical variables have the number of sites with presence of the category listed instead of the range and units.

Category	Variable	Description	Range	Units
climate	Pmin	mean monthly precipitation of the driest month of the year	7-96	mm
climate	Pmax	mean monthly precipitation of the wettest month of the year	28-273	mm
climate	Tmax	mean monthly temperature of the hottest month of the year	15.5-31.9	°C
climate	Tmin	mean monthly temperature of the coldest month of the year	-18.8--3.1	°C
climate	Gdays	mean number of annual growing days (days between first and last freeze)	10-176	days
disturbance	Fire	presence of fire within last 10 years	191 of 1329 sites	
disturbance	Grazing1k	percent of 1-km buffer around site with grazing allotments	0-100	%
disturbance	GrazingSite	presence of grazing allotments	783 of 1329 sites	
disturbance	Rd1k	length of roads in 1-km buffer around site	0-30408	m
disturbance	RdNear	distance from site to nearest road	0.29-19220	m
geology, soil, nutrient	RockP	percent phosphorous in the underlying bedrock	0.066-3.15	%
geology, soil, nutrient	RockN	percent nitrogen in the underlying bedrock	0-0.65	%
geology, soil, nutrient	Nfixer	cover of nitrogen fixing species at site	0-56	%
geology, soil, nutrient	Ndep	atmospheric nitrogen deposition	1.05-5.31	kg/ha
geology, soil, nutrient	OM	percent of fines composed of organic matter	1.16-10.78	%
geology, soil, nutrient	pH	pH of site	5.083-8.46	
land cover	Shrub	cover of shrubland at site	0-92	%
Land cover	Grass	cover of grassland at site	0-100	%
hydrologic	Slope	slope of site stream segment	0-25.5	%
hydrologic	Baseflow	stream flow attributed to ground-water discharge into streams	31-89	%

Table 3.3. Model performance for Random Forest models of the presence of 11 invasive plant species. See Table 3.1 for a list of species and Table 3.2 for variable descriptions.

Accuracy Measure	BRTE	CEBI	CIAR	CIVU	CYOF	ELRE	HYPE	LEVU	PHAR	RAAC	TAVU
PCC	75.0	65.1	58.6	63.0	66.6	66.7	76.1	67.1	67.4	66.9	75.2
Specificity	75.0	64.6	57.2	62.8	66.4	66.8	75.9	66.5	66.9	66.8	75.1
Sensitivity	75.8	74.2	64.3	65.0	73.3	64.2	83.8	78.3	71.2	70.3	78.4
AUC	0.823	0.769	0.662	0.701	0.790	0.706	0.873	0.803	0.764	0.728	0.835

Table 3.4. Relationship between presence of 11 invasive plant species and predictor variables based on Random Forest distribution models. Variable direction is based on visual assessment of partial dependence plots, with “+” indicating a positive relationship, “-“ negative, “f” flat and “?” unclear. The relative importance of each variable follows the variable direction in parenthesis. This measure is the mean decrease in accuracy of that variable divided by the highest mean decrease in accuracy value for that species. See Table 3.1 for a list of species and Table 3.2 for variable descriptions.

Variable	BRTE	CEBI	CIAR	CIVU	CYOF	ELRE	HYPE	LEVU	PHAR	RAAC	TAVU
Pmin	- (0.98)	? (0.8)	- (1)	- (0.89)	- (1)	- (0.97)	+ (0.82)	- (1)	+ (0.81)	- (0.78)	+ (1)
Pmax	- (1)	? (0.74)	- (0.98)	- (0.89)	- (0.89)	- (0.88)	+ (0.69)	- (0.78)	- (0.73)	- (0.81)	+ (0.94)
Tmax	+ (0.98)	+ (1)	+ (0.9)	+ (1)	+ (0.7)	+ (0.75)	+ (0.66)	+ (0.84)	+ (1)	+ (0.94)	+ (0.85)
Tmin	+ (0.9)	+ (0.83)	f (0.8)	f (0.88)	+ (0.67)	? (1)	+ (1)	+ (0.98)	+ (0.93)	+ (0.69)	+ (0.91)
Gdays	- (0.64)	+ (0.63)	+ (0.88)	+ (0.71)	+ (0.66)	f (0.65)	+ (0.55)	+ (0.59)	+ (0.98)	? (1)	+ (0.61)
Fire	+ (0.45)	+ (0.16)	+ (0.09)	+ (0.41)	+ (0.1)	+ (0.3)	+ (0.03)	+ (0.06)	+ (0.01)	f (0.05)	f (-0.04)
Grazing1k	f (0.37)	- (0.53)	f (0.26)	+ (0.53)	+ (0.53)	f (0.31)	- (0.25)	+ (0.54)	- (0.71)	+ (0.34)	- (0.59)
GrazingSite	+ (0.33)	- (0.37)	f (0.23)	f (0.28)	+ (0.4)	+ (0.15)	- (0.21)	+ (0.46)	- (0.49)	+ (0.29)	- (0.55)
Rd1k	f (0.66)	+ (0.38)	+ (0.65)	+ (0.71)	+ (0.57)	+ (0.59)	- (0.44)	+ (0.62)	+ (0.6)	+ (0.35)	+ (0.72)
RdNear	- (0.36)	- (0.35)	? (0.51)	- (0.66)	- (0.5)	- (0.52)	? (0.34)	- (0.2)	- (0.66)	- (0.31)	- (0.19)
RockP	+ (0.34)	? (0.51)	+ (0.75)	+ (0.43)	+ (0.51)	+ (0.66)	+ (0.49)	+ (0.66)	+ (0.47)	+ (0.41)	- (0.6)
RockN	+ (0.16)	+ (0.23)	+ (0.26)	+ (0.06)	+ (0.13)	+ (0.86)	+ (-0.09)	+ (0.09)	+ (0.14)	+ (0.31)	+ (0.06)
Nfixer	+ (0.37)	+ (0.54)	+ (0.33)	+ (0.18)	+ (0)	+ (0.28)	+ (-0.01)	+ (0.41)	+ (0.4)	+ (0.24)	+ (-0.04)
Ndep	- (0.75)	+ (0.7)	+ (0.9)	- (0.72)	f (0.88)	- (0.73)	+ (0.78)	+ (0.32)	+ (0.83)	+ (0.51)	+ (0.61)
OM	f (0.61)	- (0.58)	f (0.62)	+ (0.37)	+ (0.77)	- (0.63)	+ (0.72)	+ (0.68)	- (0.3)	- (0.12)	+ (0.7)
pH	+ (0.77)	f (0.72)	f (0.57)	+ (0.73)	+ (0.82)	- (0.73)	- (0.65)	f (0.9)	f (0.62)	+ (0.78)	+ (0.57)
Shrub	+ (0.56)	+ (0.44)	+ (0.63)	+ (0.49)	+ (0.28)	+ (0.37)	f (0.29)	+ (0.47)	+ (0.5)	+ (0.18)	+ (0.03)
Grass	+ (0.81)	+ (0.48)	+ (0.77)	+ (0.68)	+ (0.66)	+ (0.6)	f (0.29)	+ (0.74)	+ (0.56)	+ (0.52)	+ (0.55)
Slope	+ (0.33)	+ (0.24)	- (0.49)	+ (0.33)	+ (0.25)	? (0.19)	? (0.43)	+ (0.48)	- (0.73)	- (0.47)	? (0.49)
Baseflow	+ (0.58)	? (0.36)	f (0.81)	? (0.67)	- (0.79)	? (0.6)	- (0.66)	- (0.69)	- (0.47)	- (0.63)	- (0.38)

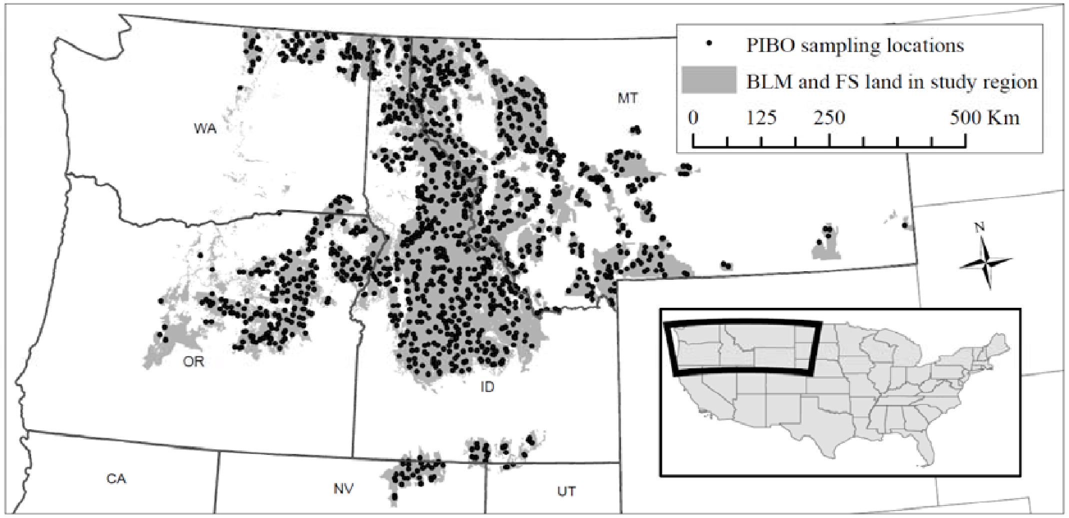

Figure 3.1. Study area and sampling locations for the USFS PIBO Effectiveness Monitoring Program. All sites are located on federally owned Bureau of Land Management and Forest Service land.

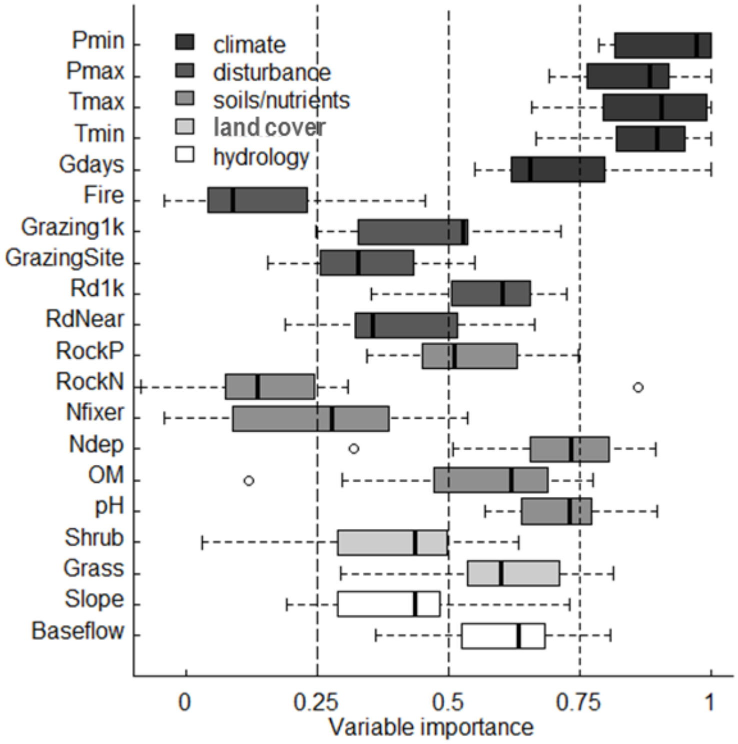

Figure 3.2. Boxplots of variable importance of predictor variables across Random Forest distribution models for 11 invasive plant species. Variable importance values of 1.00 indicate that a particular variable had the greatest contribution to the distribution model of a species, whereas values of 0.50 have half the contribution of the top variable. See Methods for more information about calculating these values. Boundary of boxes indicate the first and third quartiles, solid lines mark the medians, and whiskers indicate data beyond 1.5 times the interquartile range.

CHAPTER 4

CONCLUSIONS

This project set out to inform both theoretical and applied aspects of invasion ecology using species distribution models. In Chapter 2, we addressed the question of whether invasive species are less at equilibrium than native species and looked at drivers of *Phalaris arundinacea* invasion in order to inform management decisions for this aggressive invader. We evaluated the assumption of equilibrium by comparing model accuracy for distribution models with and without a dispersal constraint for the invasive riparian plant *P. arundinacea* and the functionally similar native *Calamagrostis canadensis.* Non-dispersal models of the native species were more accurate than models of the invasive species and incorporating a dispersal constraint improved model fit more for the invasive species than for the native species. Together these results support the hypothesis that introduced species are further from equilibrium than native species. Two insights were highlighted by our results. First, the overall improvement in model fit with the dispersal constraint was relatively low for both species. This may reflect the coarse nature of the dispersal constraint used in our models. Alternatively, niche-only models may be adequate for modeling the distribution of at least some invasive species. Comparison of the effectiveness of different methods for quantifying dispersal potential could help separate these possibilities. The second insight from our study is that incorporating dispersal processes can improve model results for both introduced *and* native species. There may be some native species that show greater improvement than that seen in our study since the degree to which environmental and dispersal factors control distributions probably varies among species (Leathwick 2009).

We used four different distribution modeling techniques to model our study species. Results from these models showed general consistency in the selected final predictor variables and the direction of the relationship between predictor variables and the presence of the species of interest. *Phalaris arundinacea* is more likely to be found in hotter areas, particularly if there is also adequate summer rainfall. Ongoing climate change may increase or at least shift the area susceptible to invasion. However, our results may be strain-specific since winter tolerance and other physiological traits can vary between source populations of *P. arundinacea* (Klebesadel & Dofing 1991; Sahramaa & Jauhiainen 2003). Another important relationship we found was that *P. arundinacea* is more likely to invade sites with increased nitrogen levels. This result agrees with experimental evidence (Wetzel & Valk 1998; Kercher & Zedler 2004) and extends this knowledge by showing a response to both natural nitrogen levels from nitrogen-fixing species and anthropogenic sources from nitrogen deposition. Restoration projects should employ careful species selection, including use of native species with high carbon to nitrogen ratios and avoidance of nitrogen-fixers, if they seek to limit *P. arundinacea* invasion. We found that one type of disturbance, namely roads, increased site susceptibility to invasion, while *P. arundinacea* was less likely to be found in areas with livestock grazing. Species control along roadsides could be a valuable tool for preventing the spread of this species. The relationship between *P. arundinacea* and grazing should be evaluated further since it agrees with other observational studies (Paine & Ribic 2002), but contradicts experimental work (Kercher & Zedler 2004).

In Chapter 3, we examined what types of attributes make sites susceptible to invasion by 11 plant species in riparian areas in the northwestern United States and whether the relationships between site attributes and invasion were species-specific or more general. We found that factors related to climate, soil, and nutrient conditions were more important for predicting the distributions of invasive plant species than land cover or factors related to disturbance. This validates the idea that invasion occurs as a series of stages with filters determining progress from one stage to the next and climate and/or abiotic conditions serving as the first filters after a species is initially introduced to a broad region (Theoharides & Dukes 2007). We also found that there was a general pattern related to invasion for most species. Invasion was more likely at hot dry sites near roads with high grass or shrub cover and high nutrient levels along streams with lower baseflow values. Roads may promote invasion both by increasing dispersal opportunities and providing conditions that aid establishment. The remaining attributes related to site invasibility may be related to resource opportunities, *sensu* Shea and Chesson (2002). Sites with high baseline nutrients levels, less shading, and occasional pulses of water from precipitation or stream flow may provide a window of opportunity for invaders to establish. There was some heterogeneity in how factors affected site invasion risk for particular species. For example, the response to livestock grazing was almost equally divided between species more and less likely to be found near grazing allotments. Based on our results, we identified three major management needs to help lower invasion risk in our study area: nutrient management, monitoring and prevention measures along roadways, and long-range planning for climate change. These management actions will help lower site susceptibility to invasion by most of our study species. Species-specific management strategies can complement our recommendations in areas prone to particular species.

In our studies, we demonstrated the utility of species distribution models to address both theoretical and applied questions. We found evidence that introduced species are less likely to be at equilibrium than native species, suggesting that dispersal processes and lag phases need greater emphasis in studies of invasion. We also found that similar characteristics make sites vulnerable to invasion by a suite of plant species, lending support to theories of site invasibility. Management recommendations for our model invasive species, *P. arundinacea*¸ and for the study region as a whole are similar. Actions that mitigate the effects of roads, nutrient levels, and climate change are likely to lower invasion risk in our study area.

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APPENDICES

Appendix A. Partial dependence plots for variables in the final Random Forest and Boosted Tree models of *Calamagrostis canadensis* and *Phalaris arundinacea*.

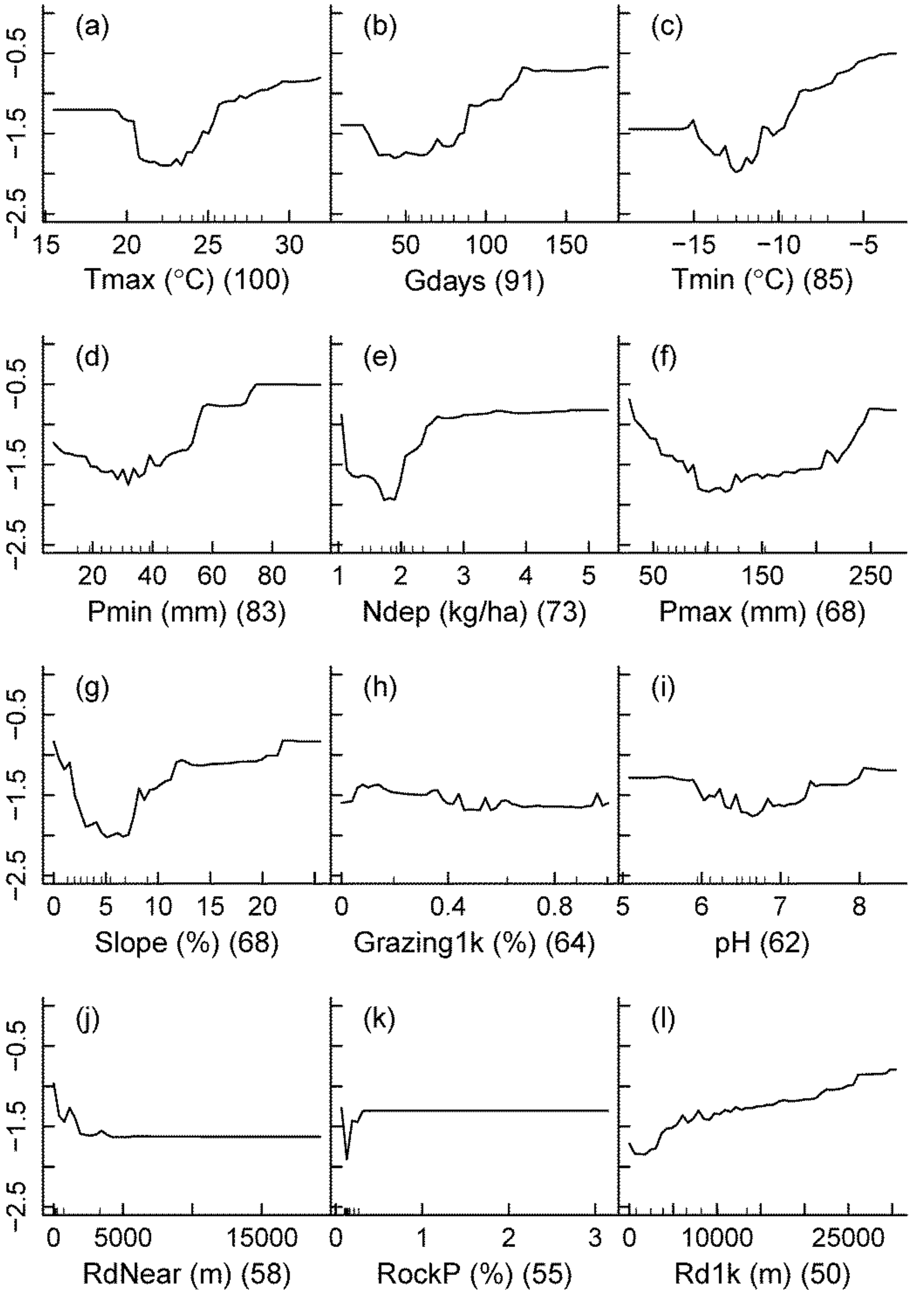

Figure A.1. Partial dependence plots for variables in the final Random Forest model of *Phalaris arundinacea* presence. Normalized variable importance measure follows variables units. Small ticks on the x-axis indicate deciles of the variables. See Table 2.1 for variable descriptions.

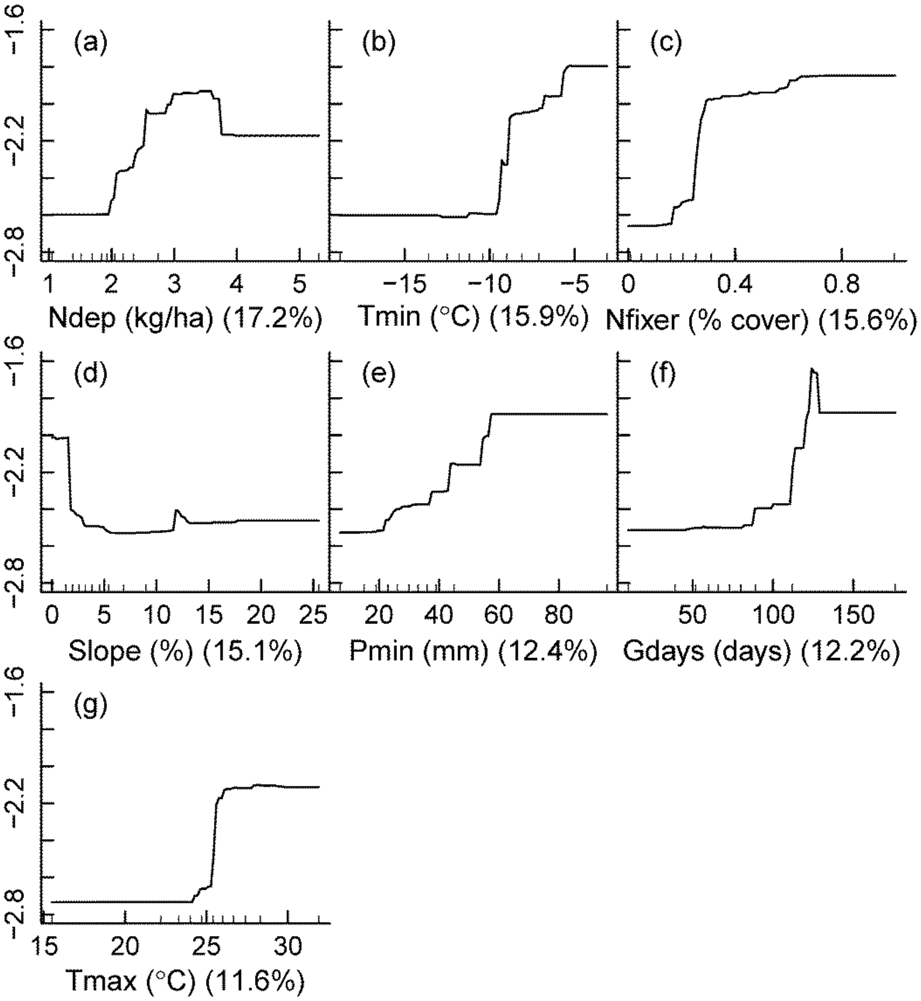

Figure A.2. Partial dependence plots for variables in the final Boosted Tree model of *Phalaris arundinacea* presence. Relative percent contribution of each variable to predicting species presence follows variables units. Small ticks on the x-axis indicate deciles of the variables. See Table 2.1 for variable descriptions.

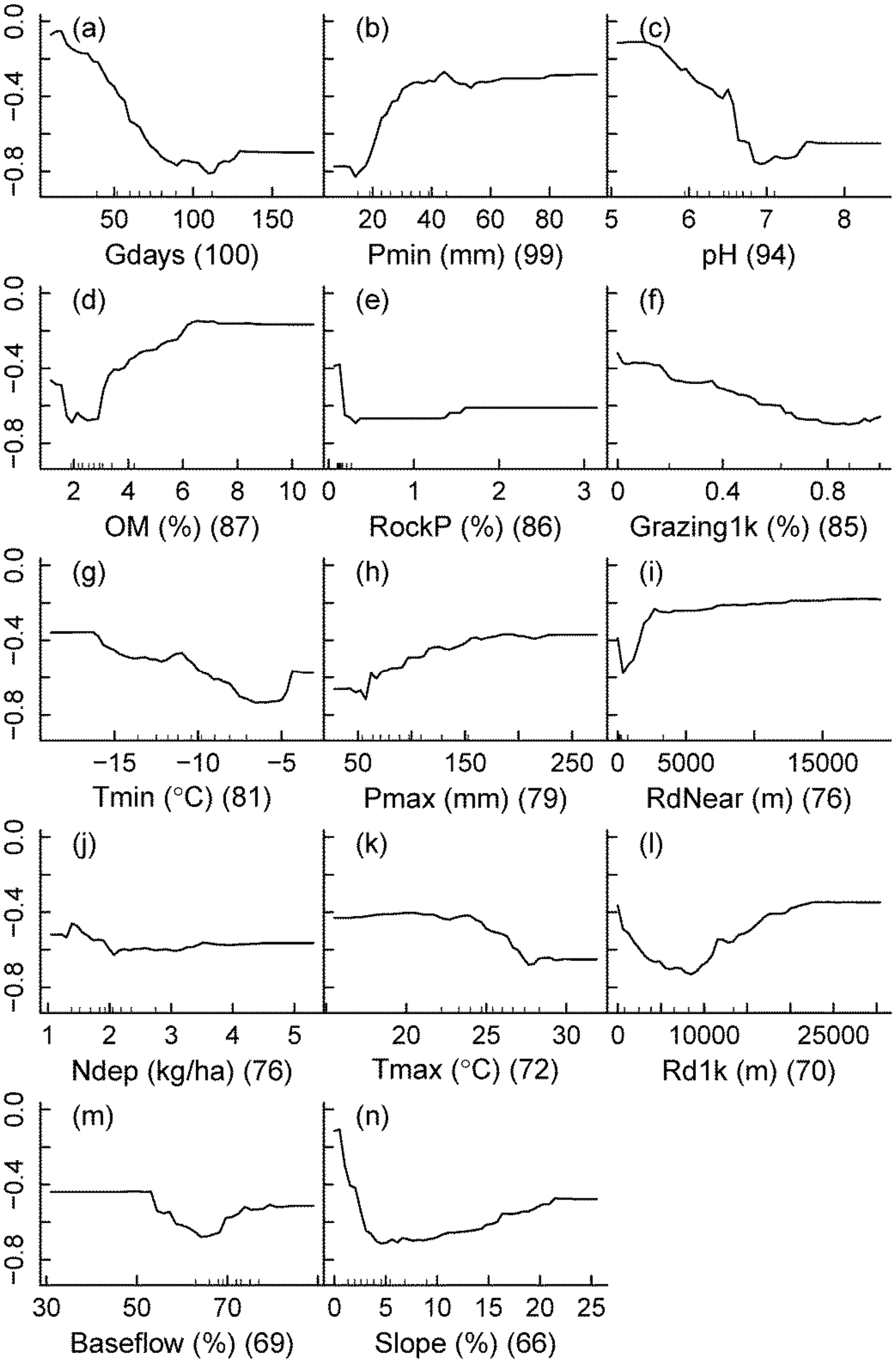

Figure A.3. Partial dependence plots for variables in the final Random Forest model of *Calamagrostis canadensis* presence. Normalized variable importance measure follows variables units. Small ticks on the x-axis indicate deciles of the variables. See Table 2.1 for variable descriptions.

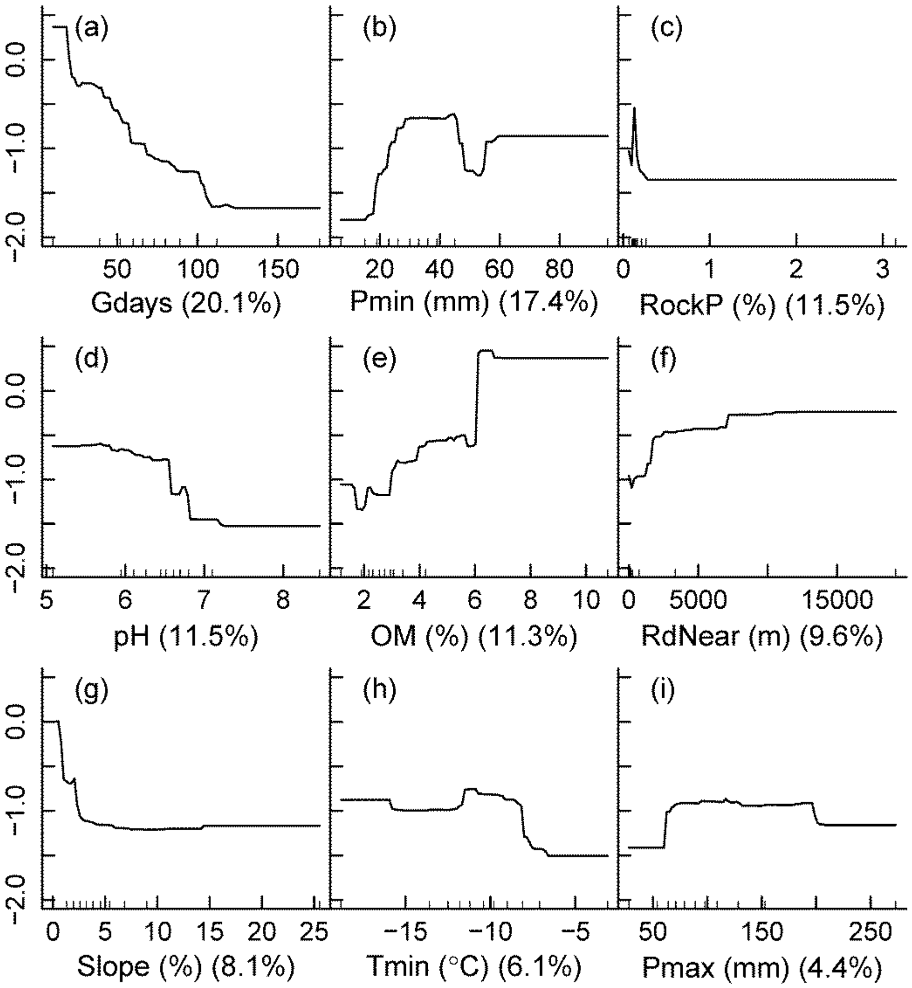

Figure A.4. Partial dependence plots for variables in the final Boosted Trees model of *Calamagrostis canadensis* presence. Relative percent contribution of each variable to predicting species presence follows variable units. Small ticks on the x-axis indicate deciles of the variables. See Table 2.1 for variable descriptions.

Appendix B. Partial dependence plots for variables in Random Forest models of 11 invasive plant species.

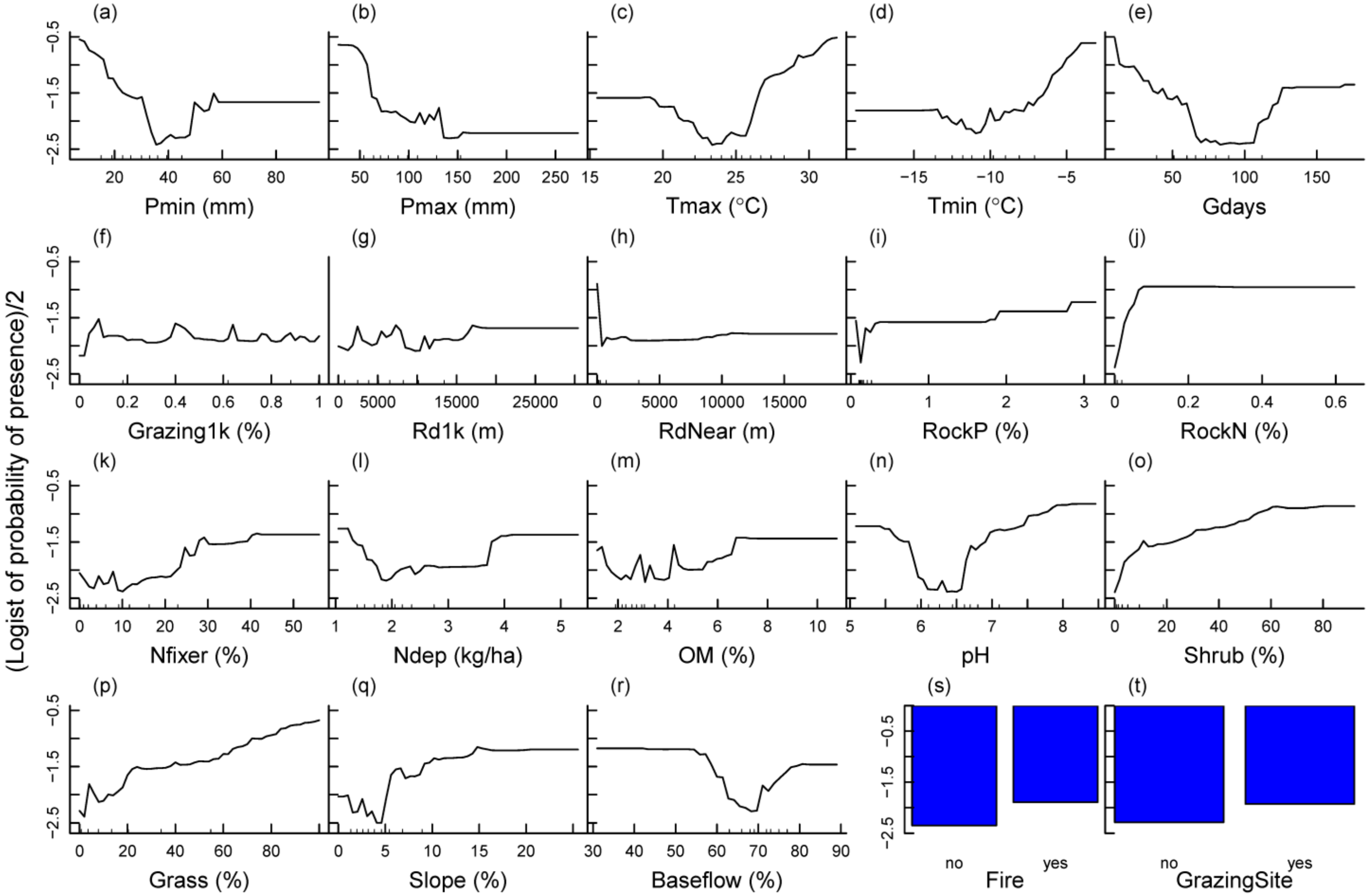

Figure B.1. Partial dependence plots for variables in the Random Forest model of *Bromus tectorum* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

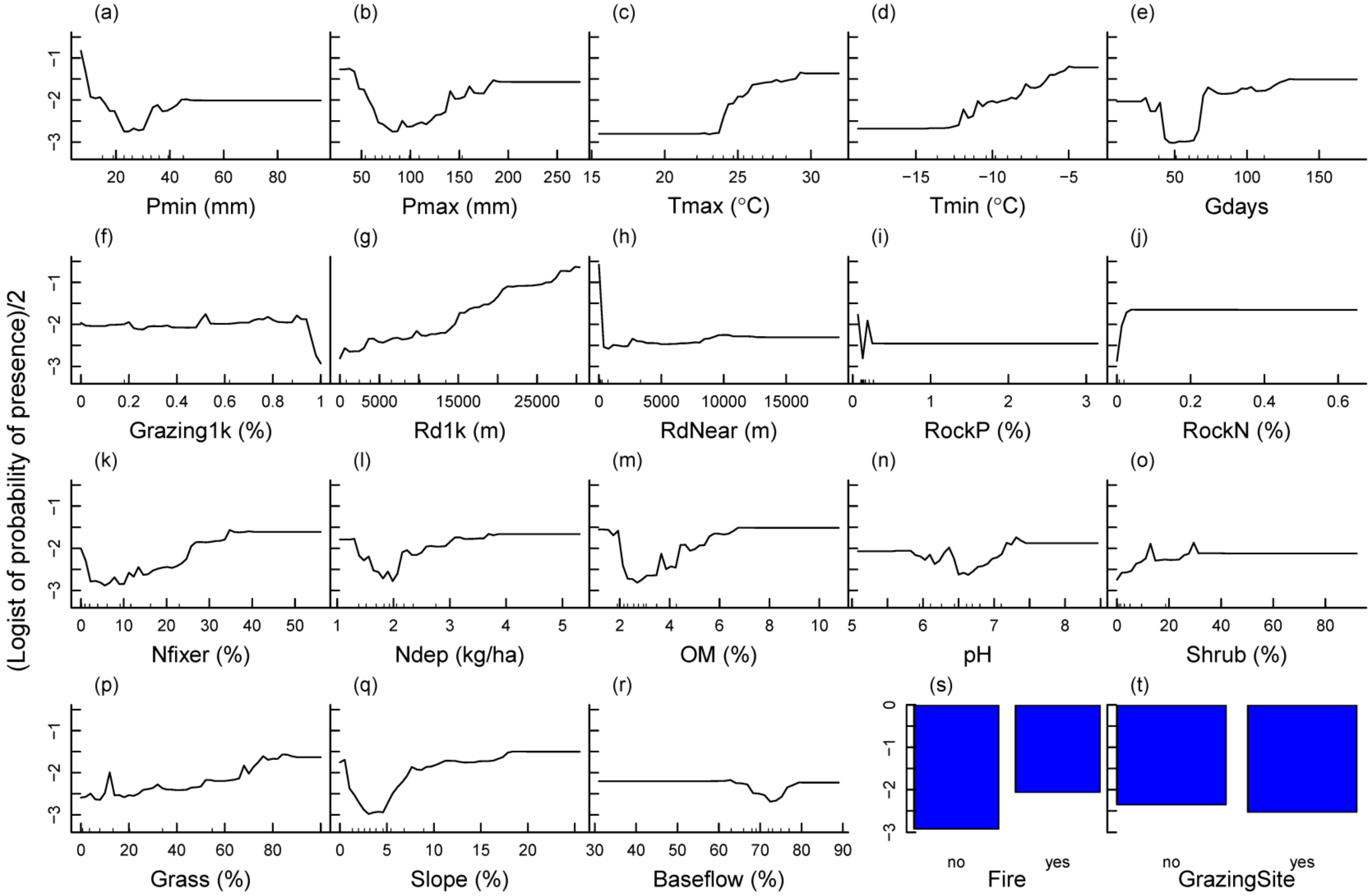

Figure B.2. Partial dependence plots for variables in the Random Forest model of *Centaurea biebersteinii* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

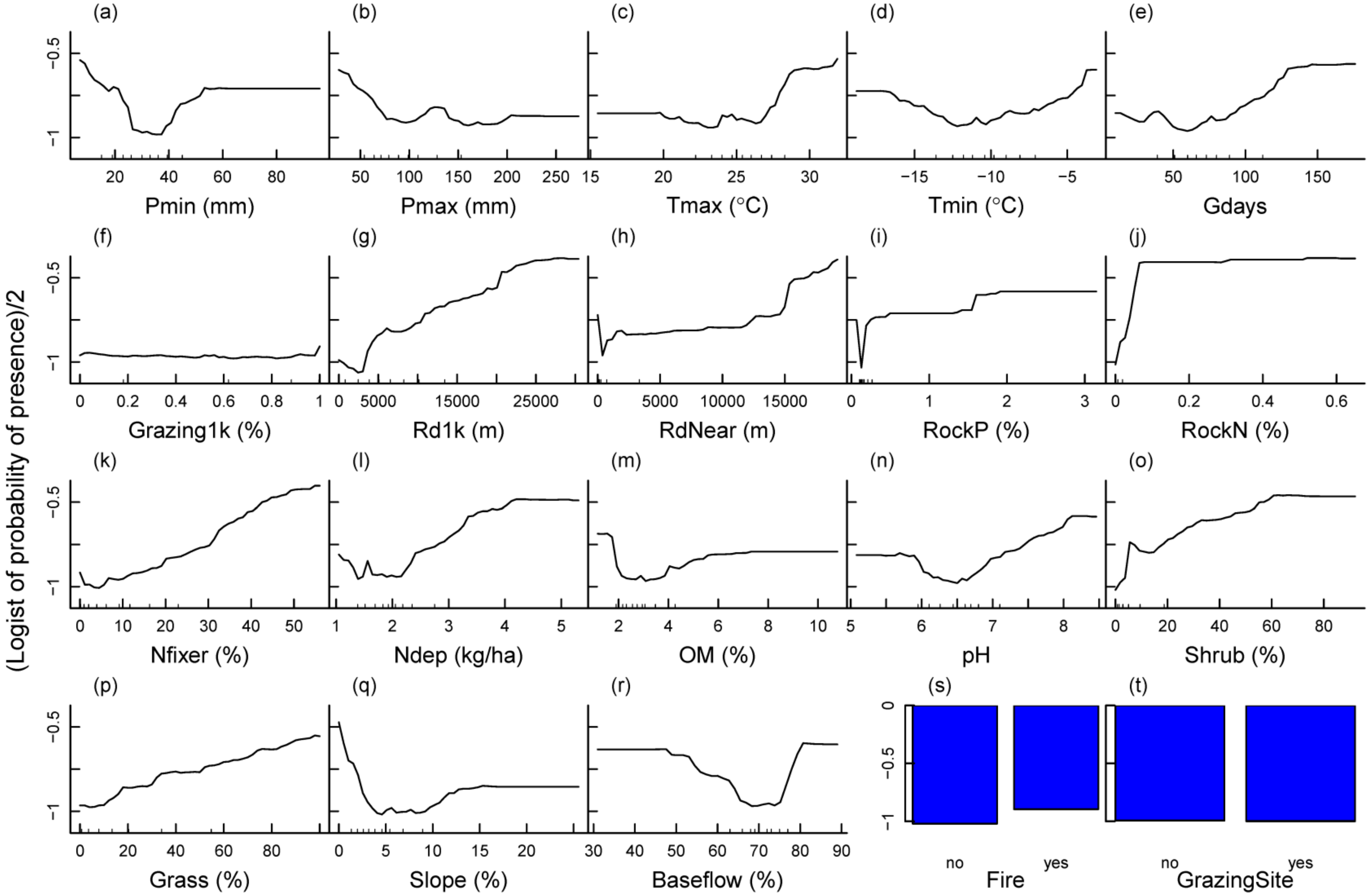

Figure B.3. Partial dependence plots for variables in the Random Forest model of *Cirsium arvense* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

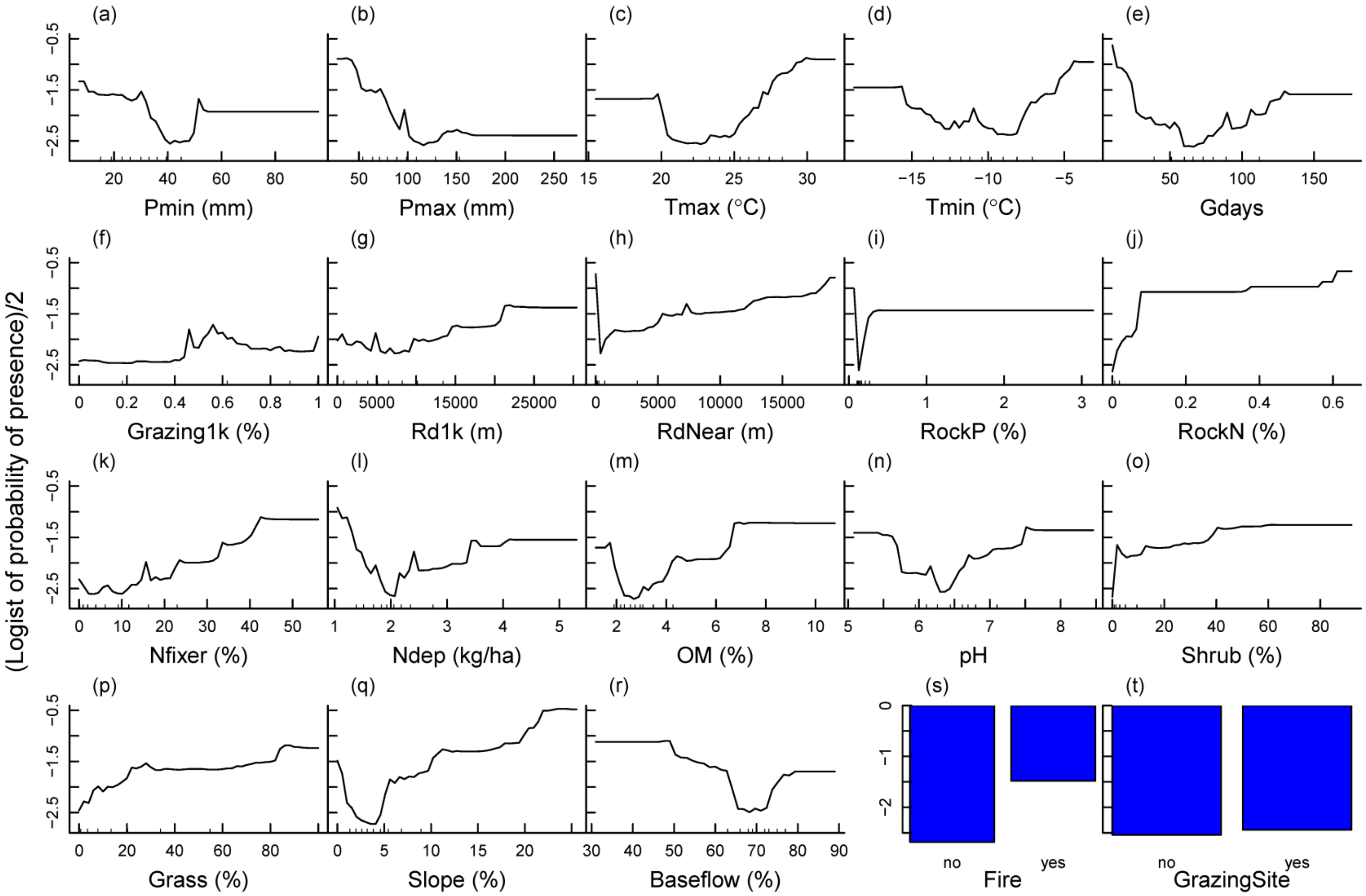

Figure B.4. Partial dependence plots for variables in the Random Forest model of *Cirsium vulgare* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

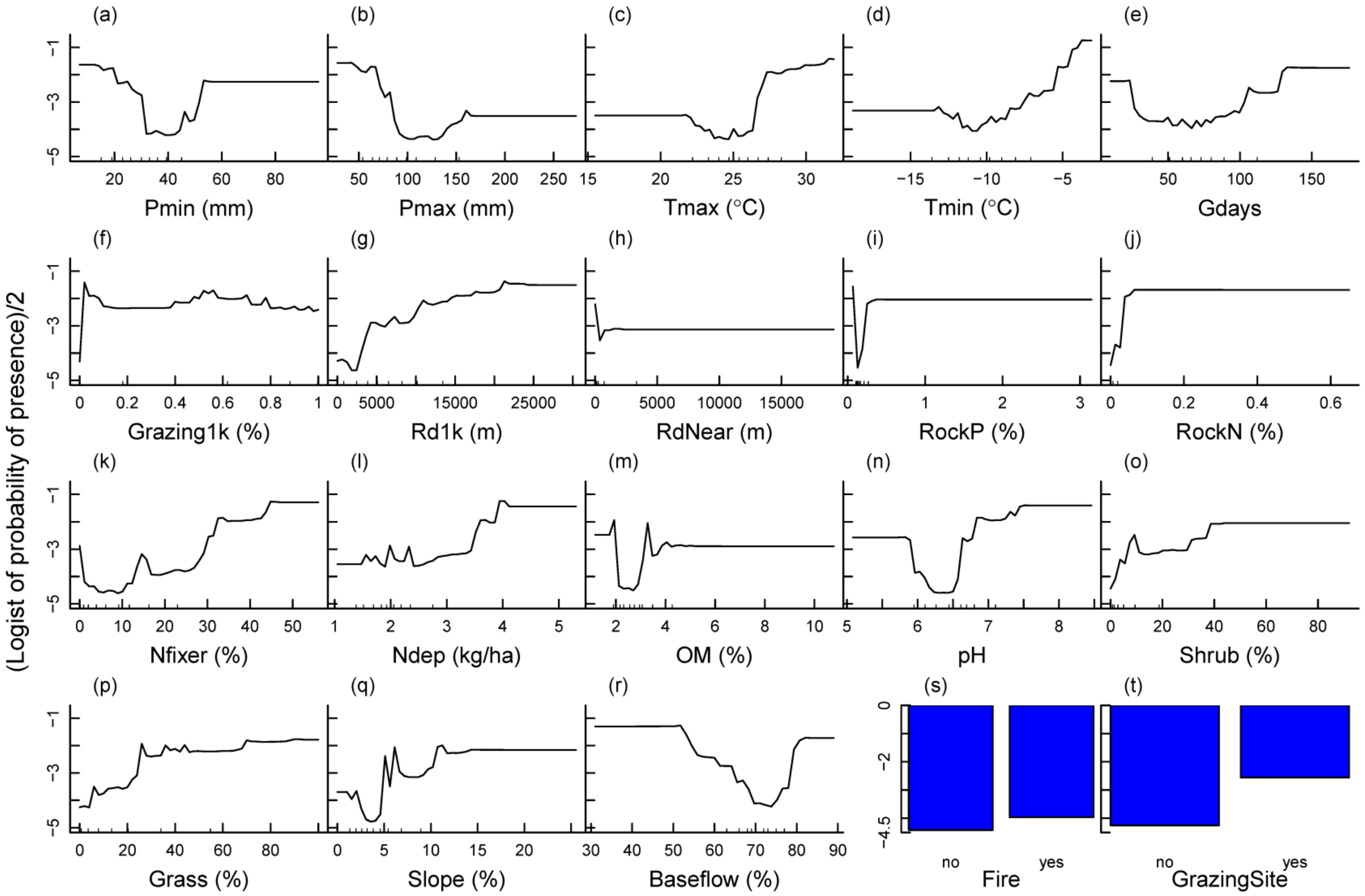

Figure B.5. Partial dependence plots for variables in the Random Forest model of *Cynoglossum officinale* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

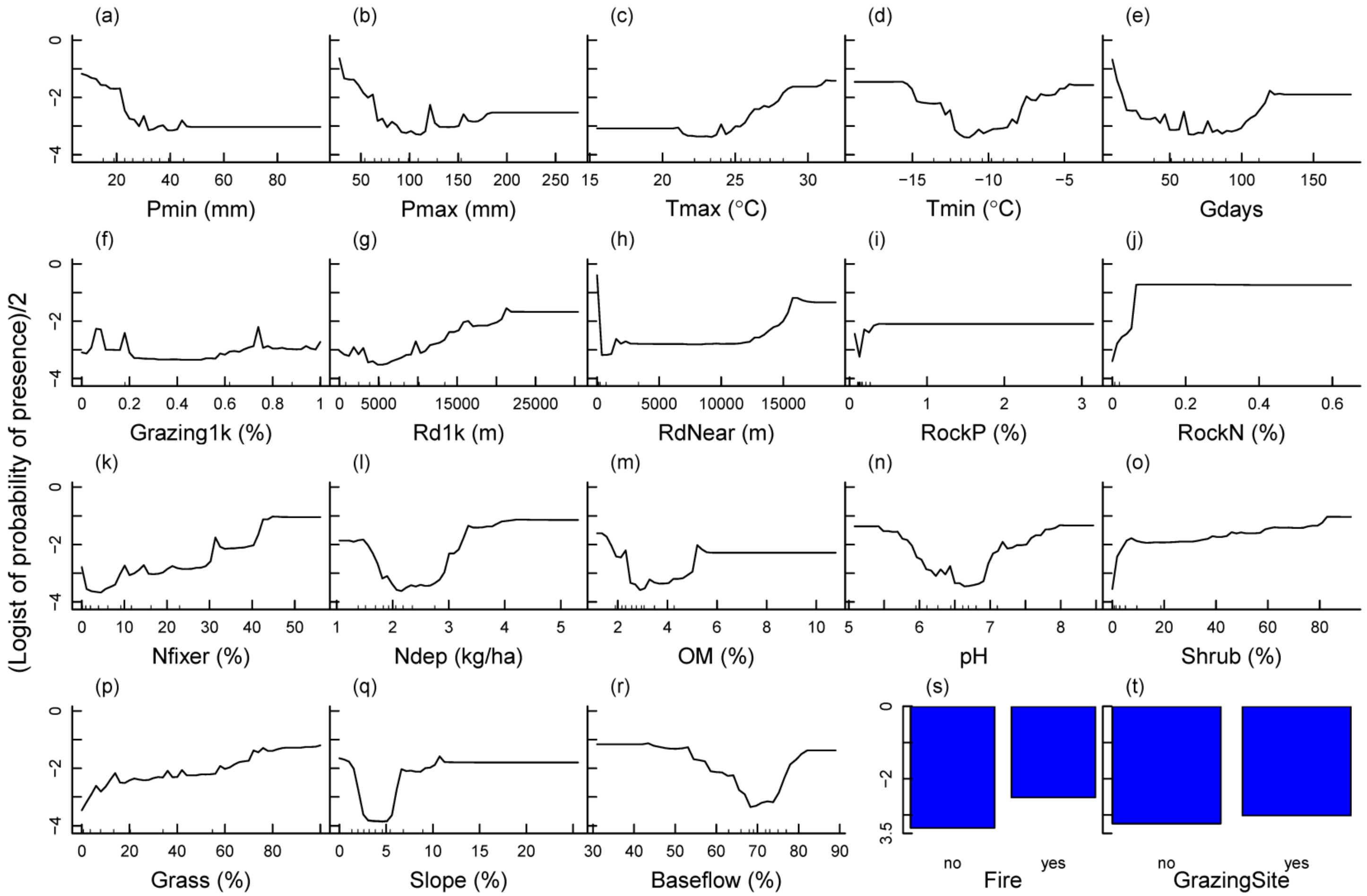

Figure B.6. Partial dependence plots for variables in the Random Forest model of *Elymus repens* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

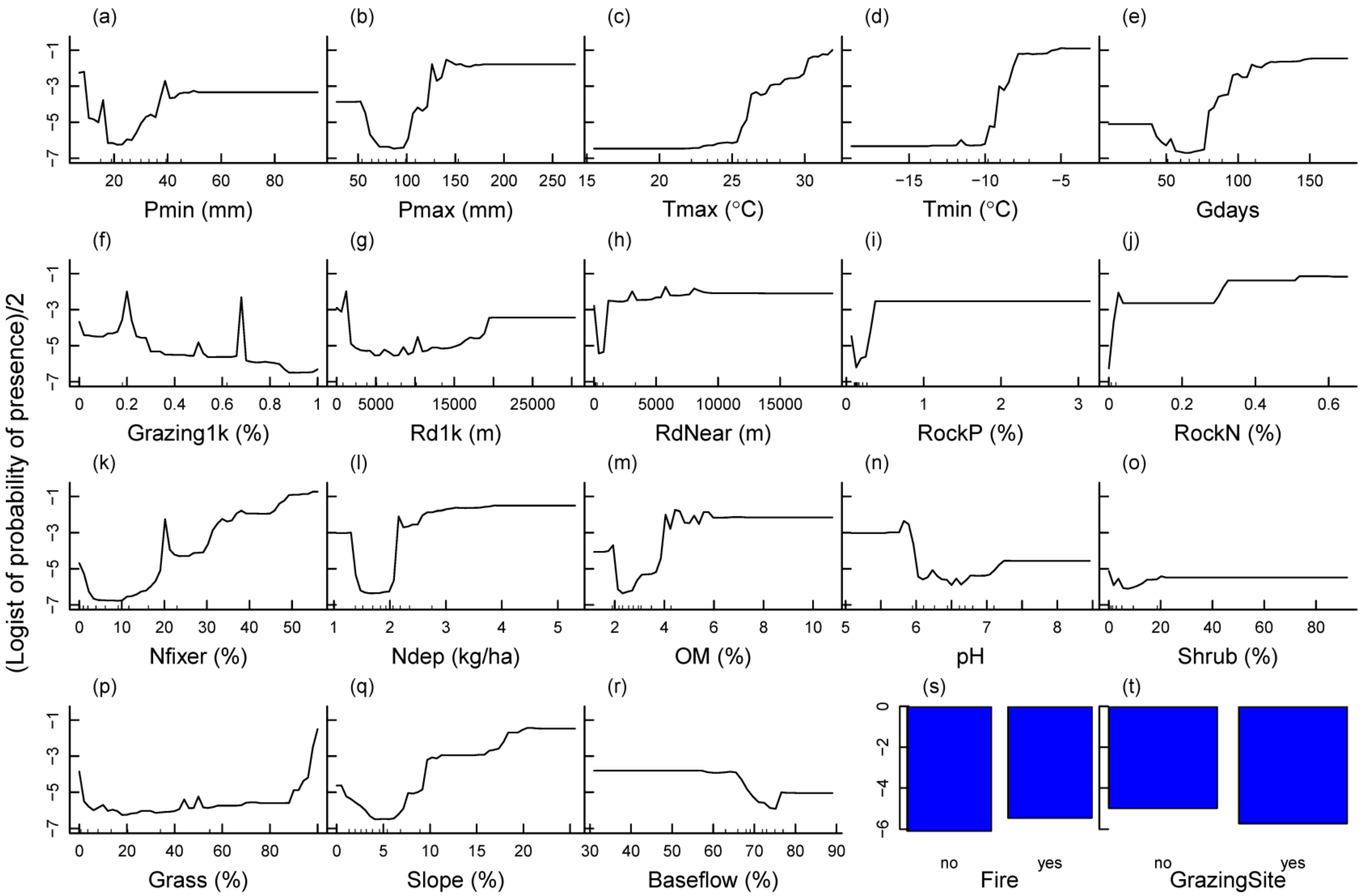

Figure B.7. Partial dependence plots for variables in the Random Forest model of *Hypericum perforatum* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

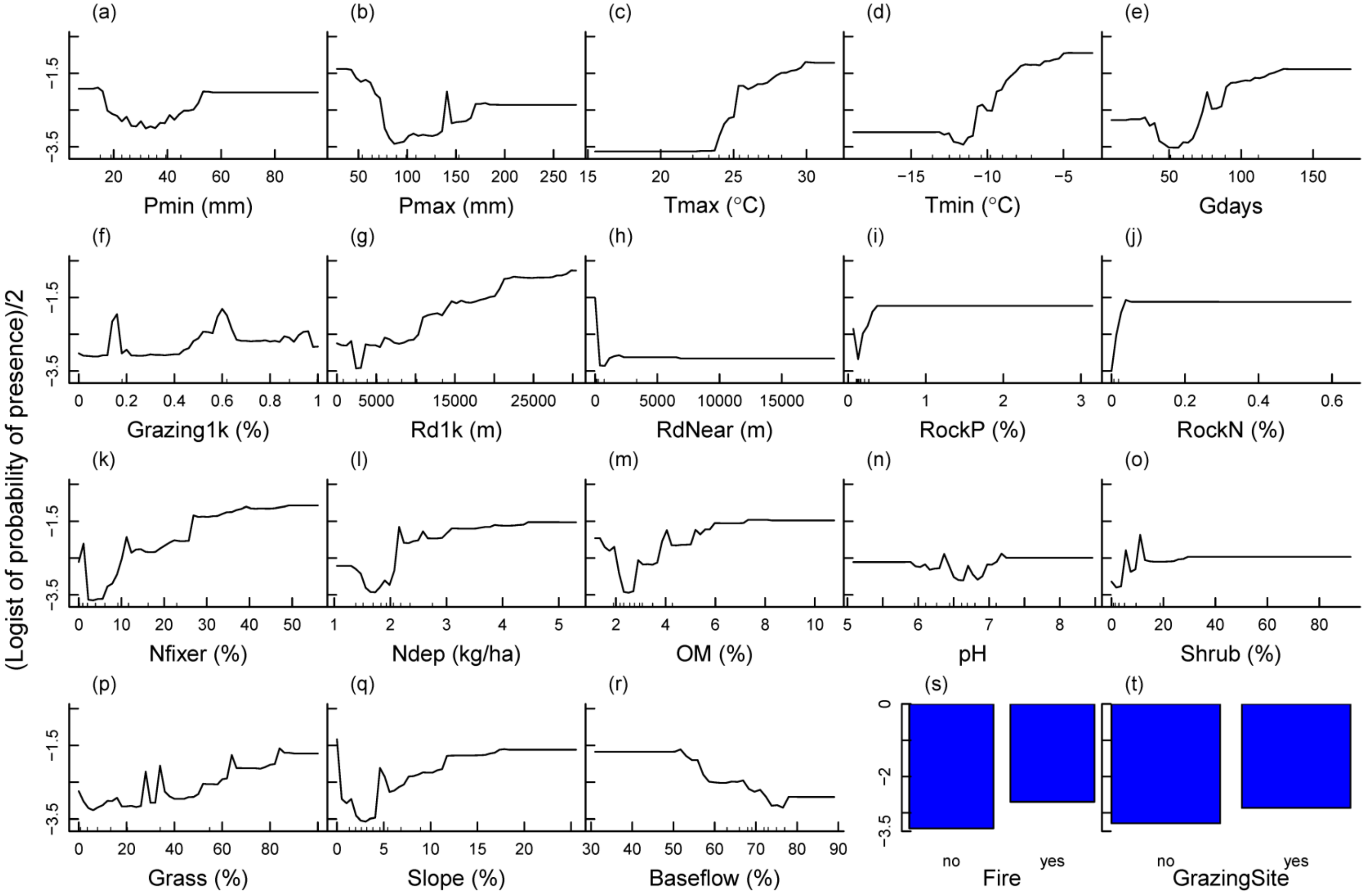

Figure B.8. Partial dependence plots for variables in the Random Forest model of *Leucanthemum vulgare* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

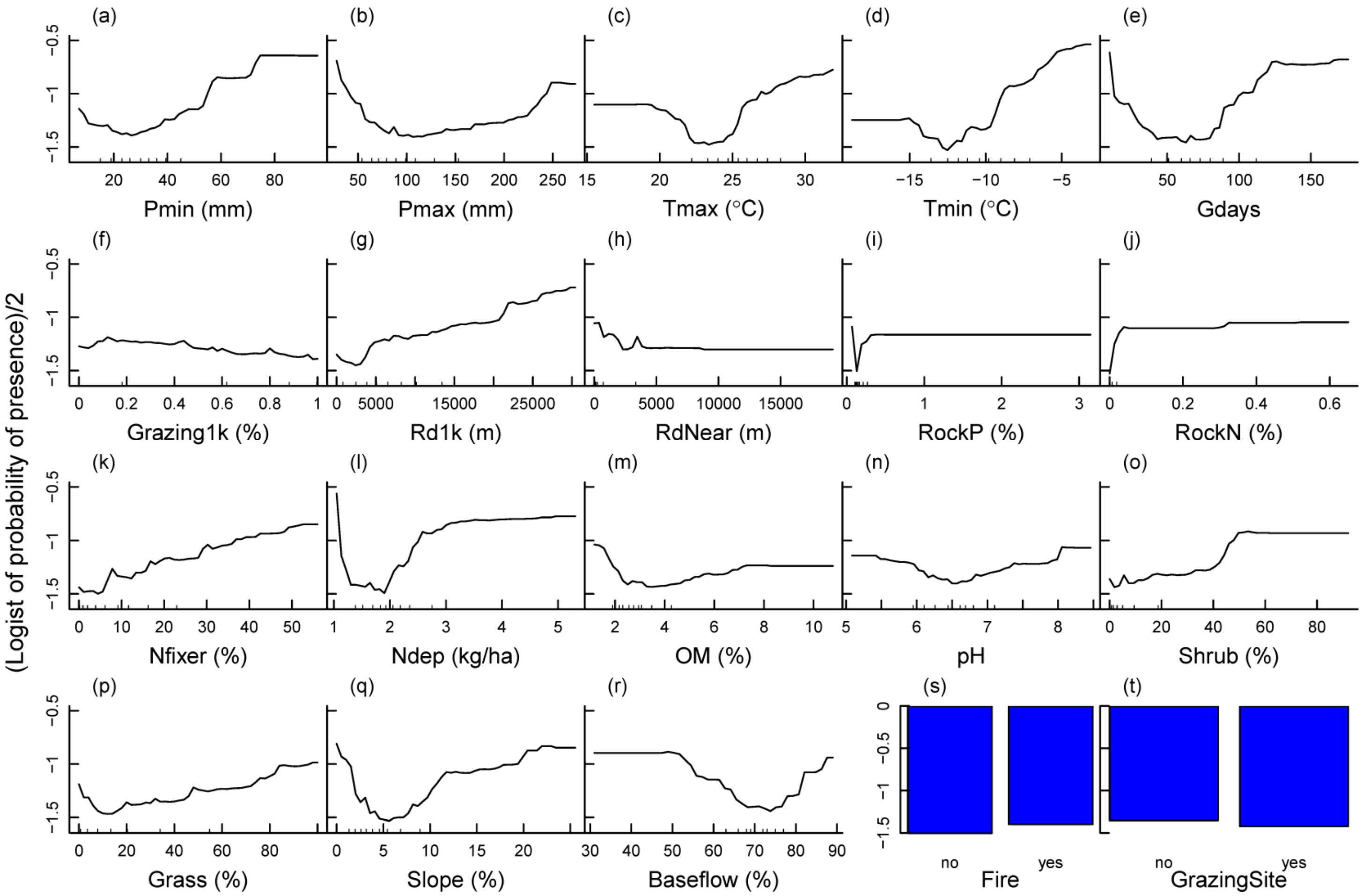

Figure B.9. Partial dependence plots for variables in the Random Forest model of *Phalaris arundinacea* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

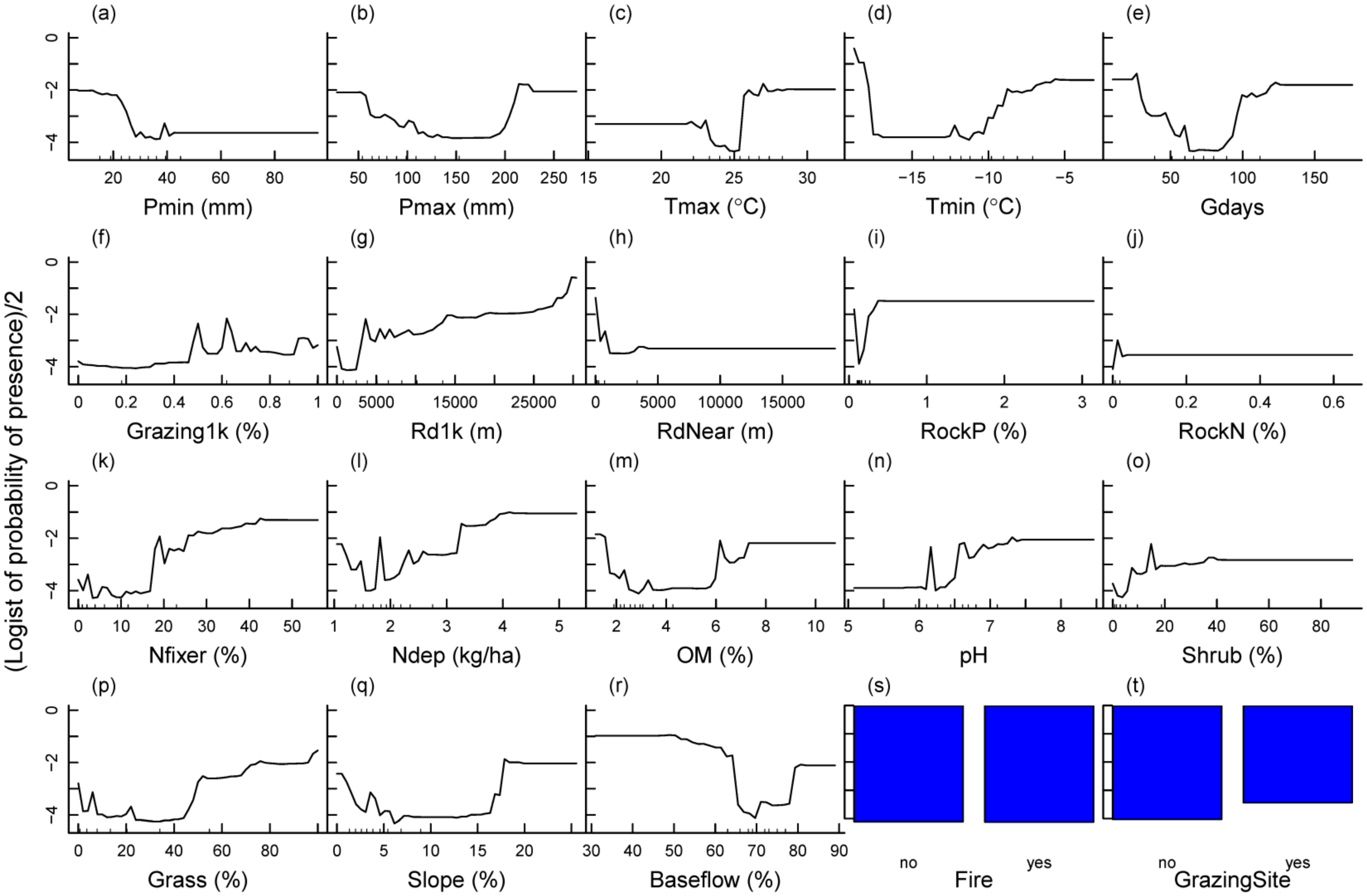

Figure B.10. Partial dependence plots for variables in the Random Forest model of *Ranunculus acris* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.

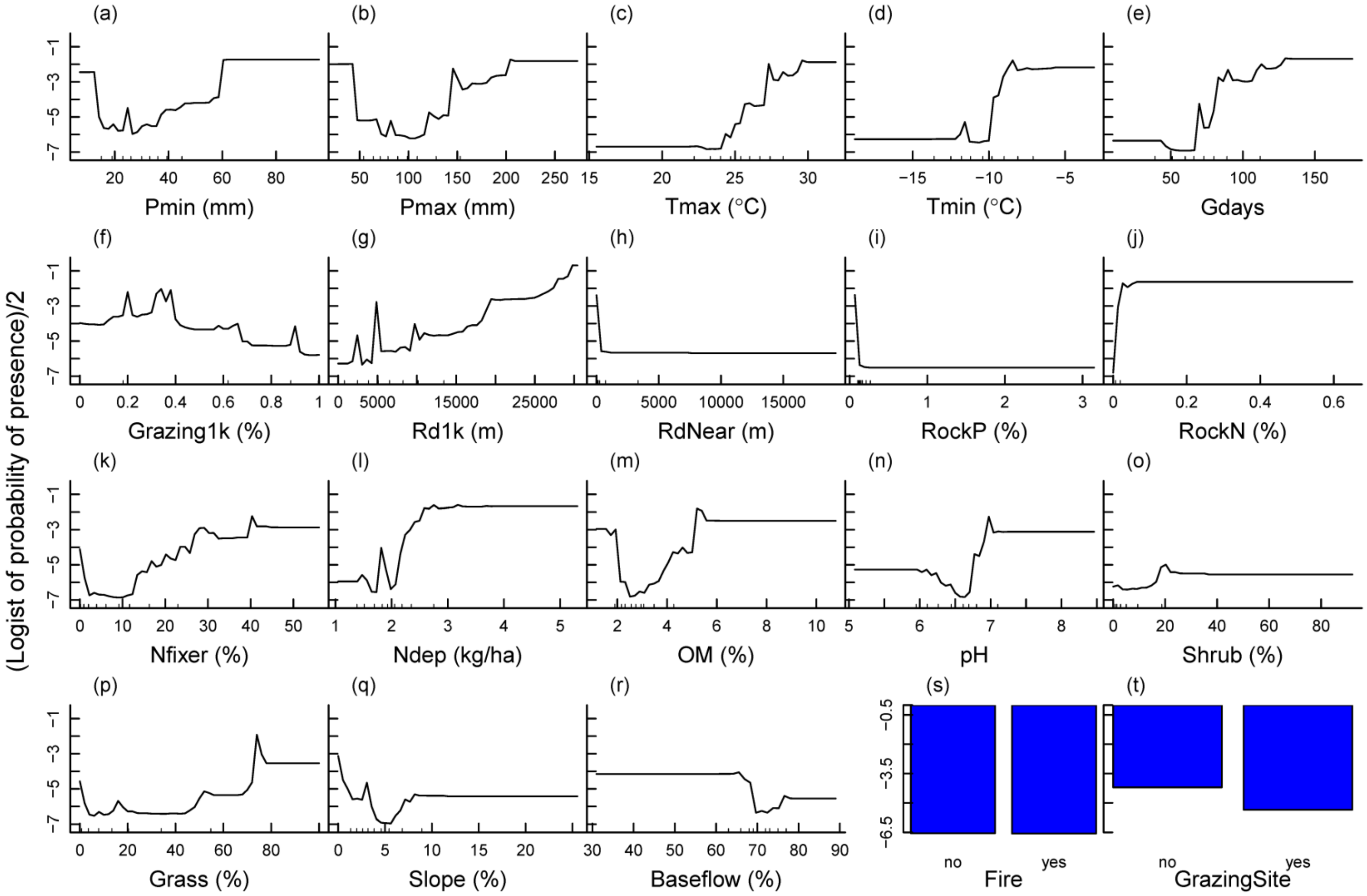

Figure B.11. Partial dependence plots for variables in the Random Forest model of *Tanacetum vulgare* presence. Small ticks on the x-axis indicate deciles of the variables. See Table 3.2 for variable descriptions.