Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity

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Abstract

Interactions between climate change and non-native invasive species may combine to increase invasion risk to native ecosystems. Changing climate creates risk as new terrain becomes climatically suitable for invasion. However, climate change may also create opportunities for ecosystem restoration on invaded lands that become climatically unsuitable for invasive species. Here, I develop a bioclimatic envelope model for cheatgrass (*Bromus tectorum*), a non-native invasive grass in the western US, based on its invaded distribution. The bioclimatic envelope model is based on the Mahalanobis distance using the climate variables that best constrain the species' distribution. Of the precipitation and temperature variables measured, the best predictors of cheatgrass are summer, annual, and spring precipitation, followed by winter temperature. I perform a sensitivity analysis on potential cheatgrass distributions using the projections of 10 commonly used atmosphere–ocean general circulation models (AOGCMs) for 2100. The AOGCM projections for precipitation vary considerably, increasing uncertainty in the assessment of invasion risk. Decreased precipitation, particularly in the summer, causes an expansion of suitable land area by up to 45%, elevating invasion risk in parts of Montana, Wyoming, Utah, and Colorado. Conversely, increased precipitation reduces habitat by as much as 70%, decreasing invasion risk. The strong influence of precipitation conditions on this species' distribution suggests that relying on temperature change alone to project future change in plant distributions may be inadequate. A sensitivity analysis provides a framework for identifying key climate variables that may limit invasion, and for assessing invasion risk and restoration opportunities with climate change.

Keywords: bioclimatic envelope modeling, *Bromus tectorum*, climate change, climatic habitat, ecological niche, Mahalanobis distance, plant invasion

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Introduction

Climate change threatens to alter global ecosystems profoundly. Species occurrence is often tightly coupled to climatic conditions. A shift in temperature or precipitation may make current habitat climatically unsuitable, changing the potential distributions of species. Climate change may lead to a shift of suitable ranges to higher altitudes and/or poleward (e.g., McCarty, 2001; Walther *et al.*, 2002), loss of native species (Sala *et al.*, 2000; Thuiller *et al.*, 2005a), or even extinction (Thomas *et al.*, 2004). In addition to change the potential distributions of native species, climate changing may also affect

the spatial distributions of land at risk from invasive species (Peterson, 2003; Thuiller *et al.*, 2007).

The transformation of ecosystems by invasion of non-native species has been identified as a major component of global change (Vitousek *et al.*, 1996). Alien invaders create economic losses via direct impact on industry (e.g., agriculture, transportation) as well as through costs associated with slowing invasion and restoring invaded ecosystems (DiTomaso, 2000; Mack *et al.*, 2000). Annual costs of damage and control of plant invaders in the United States have been estimated in the billions of dollars (Pimentel *et al.*, 2000). Invasive plants also threaten native species and change ecosystem function (e.g., by altering water availability or fire frequency) (D'Antonio & Vitousek, 1992; Zavaleta, 2000). Predicting how climate change will affect biological invasions

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is a major challenge for management and conservation planning.

Potential interactions between climate change and invasive species are a recognized problem (Dukes & Mooney, 1999; Weltzin et al., 2003; Moore, 2004; Thuiller et al., 2007), but rarely have been quantified for specific regions, species, or future climate scenarios. Assessments of the impacts of climate change on invasive plants have focused on either the impacts of increased CO_2 or modeled changes in climatic suitability. Increased CO_2 positively affects the growth of some invasive plants (Sasek & Strain, 1988, 1989, 1991; Ziska, 2003), and several studies have found enhanced competitiveness in plant invaders with elevated CO_2 (Smith et al., 1987, 2000; Nagel et al., 2004), although changing competitive regimes will be species specific. These studies highlight the general risk of enhanced invasive species competitiveness with climate change; however, they do not address the biogeographic aspects of invasion risk.

Bioclimatic envelope models are used to statistically describe a species' climatic habitat (see reviews by Franklin, 1995; Guisan & Zimmermann, 2000; Pearson & Dawson, 2003; Guisan & Thuiller, 2005). Climatic habitat is described based on empirical relationships between species distributions and climate variables (Kearney, 2006). Although this approach is limited because other factors besides climate affect species distribution (Dormann, 2007), bioclimatic envelope models provide first-order estimates of both the climate variables that most constrain distribution (Hirzel et al., 2002) and the potential distribution changes associated with climate change (Pearson & Dawson, 2003; Araujo et al., 2005; Hijmans & Graham, 2006). Defining the climatic habitat is a critical component of assessing the ecological niche of invasive species and thus assessing invasion risk (Peterson, 2003).

Bioclimatic envelope models have been used to predict invasion risk under current climate conditions based on invasive species distributions in their native and/or invaded ranges (Welk et al., 2002; Rouget et al., 2004; Thuiller et al., 2005b; Mau-Crimmins et al., 2006; Schussman et al., 2006). A handful of studies have coupled bioclimatic envelope modeling with climate change to predict future distributions of invasive species (Beerling, 1993; Sutherst, 1995; Zavaleta & Royval, 2002; Kriticos et al., 2003; Mika et al., 2008). However, only Kriticos et al. (2003) and Mika et al. (2008) included precipitation change in addition to temperature change in their distribution modeling. Given the importance of water availability to plants, precipitation change needs to be included in the predictions of climate change effects on invasive plants.

Previous studies may have neglected precipitation change due to the high level of uncertainty associated with changing precipitation in coupled atmosphere–ocean general circulation models (AOGCMs) (Milly et al., 2005; Randall et al., 2007). This uncertainty is particularly problematic in the western US, where complex topography coupled with the difficulty of modeling El Niño result in highly variable climate projections. Uncertainty in AOGCM projections must be considered and incorporated into any predictions of change in species range.

In this work, I present a bioclimatic envelope model for the invasive plant cheatgrass (Bromus tectorum) in the western US. I use regional presence data to empirically derive the climate variables that best constrain species distribution. I then use these best climate predictors to model the climatic habitat under recent (late 20th century) climate conditions. Finally, I perform a sensitivity analysis on the distribution of climatic habitat by changing the climate predictor variables to extremes predicted by AOGCMs for the year 2100. This approach provides estimates of spatially extensive areas with both increased and decreased suitability for cheatgrass under future climate change conditions.

Background

Cheatgrass is an invasive annual grass that invades perennial shrublands in the western US, primarily sagebrush steppe and slightly drier salt desert shrubland characteristic of the Great Basin Desert. Cheatgrass is a Eurasian grass that was accidentally introduced to the United States in the late 1800s (Mack, 1981, 1989) and now dominates at least $40\,000\,km^2$ in the states of Nevada and Utah alone (Bradley & Mustard, 2005). Cheatgrass-dominated lands are less viable as rangeland because the senesced grass is inedible for livestock (Currie et al., 1987; Young & Allen, 1997). Furthermore, the increase in fine fuels associated with cheatgrass leads to higher incidence of fire (Whisenant, 1990; D'Antonio & Vitousek, 1992). Fires in turn lead to a virtually irreversible loss of native shrubs and grasses, which reduces ecosystem carbon storage (Bradley et al., 2006), and threatens sagebrush obligate species. Once established, cheatgrass is extremely difficult to eradicate and expansion of the species continues to be a major problem in the western US (Billings, 1990; Knapp, 1996).

Cheatgrass competes with native species by growing early in the spring season and using available water resources (Rice et al., 1992; Peterson, 2005). Cheatgrass senesces in the late spring, setting seed and remaining dormant through the summer. Native sagebrush and salt desert shrubs, on the other hand, begin growing in mid to late spring and continue to grow through the summer under favorable precipitation conditions. Hence, the phenologies of the dominant native and

invasive plant species are distinctly different, with cheatgrass relying predominantly on spring precipitation and native shrubs relying predominantly on summer precipitation (Rice *et al.*, 1992; Loik, 2007).

The Great Basin Desert, where cheatgrass is most problematic, is a semi-arid cold desert. This region is characterized by hot summers, freezing winters, and low year round precipitation. Total annual precipitation in the region ranges from 20 to 40 cm in valleys, and is higher in mountains, which typically extend over 3000 m in elevation. Precipitation rates are similar during fall, winter, and spring and lowest during the summer.

Material and methods

Regional presence of cheatgrass was based on a map for the Great Basin ecoregion, produced with remote sensing. Bradley & Mustard (2005) used Advanced Very High Resolution Radiometer (AVHRR) Pathfinder data to identify cheatgrass based on its amplified inter-annual growth response to rainfall. Relative to native shrublands, cheatgrass-dominated communities have much higher inter-annual variability in community greenness as measured with satellite time series. This inter-annual response is a result of the El Niño Southern Oscillation affecting the western US, which causes cyclical events of regional extreme precipitation. Inter-annual variability is not related to average climatic conditions.

This map was initially produced at 1 km spatial resolution for the year 1998. I down sampled the map resolution to $0.04166°$ ($\sim$ 4 km) spatial resolution using a majority filter. This projection and pixel resolution were selected to match the PRISM (Parameter-elevation Regressions on Independent Slopes Model) current climate dataset (Daly *et al.*, 2002). The spatial distribution of cheatgrass presence based on this map is shown in Fig. 1.

Although cheatgrass can be found throughout the continental US (USDA, 2007), it is only invasive in the Intermountain West, based on its prevalence, abundance, magnitude of impact, and ability to spread. The mapped distribution used here encompasses the majority of lands where cheatgrass is invasive based on this definition. The distribution map does not include portions of central Utah and eastern Washington where cheatgrass invasion is also problematic (Mack, 1981, 1989). However, the latitudinal and topographic gradients in the Great Basin create a considerable range of climate conditions that encompass the missing areas. Thus, the mapped extents provide a reasonable estimate of the range of climatic conditions susceptible to ecosystem-transforming cheatgrass invasion.
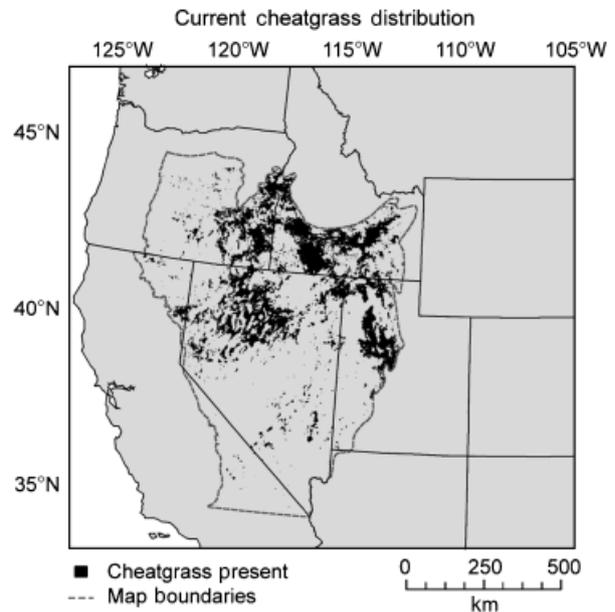

Fig. 1 Cheatgrass presence mapped using remote sensing data within the Great Basin is shown in black (Bradley & Mustard, 2005). Locations outside the extents of the Great Basin (dashed line) were not mapped and presence of cheatgrass is unknown.

Data sources current climate

Current climate conditions used to develop the bioclimatic envelope model were derived from average precipitation and temperature data from the PRISM dataset. The PRISM dataset is a 0.04166 decimal degree interpolation of US weather station data, taking into account the influence of topography on precipitation and temperature (Daly *et al.*, 2002). A total of 39 climate variables representing monthly and annual averages of precipitation, maximum temperature, and minimum temperature for the 1971–2000 time period were used in this analysis.

Data sources future climate

The application of global climate model results to regional climate modeling holds two major challenges. First, the spatial resolution of AOGCMs, commonly > 2 decimal degrees latitude (> 220 km) is coarser than current climate data. Second, although temperature increases are fairly consistent in the western US, there is a high degree of variability in climate model projections for change in precipitation (Milly *et al.*, 2005; Randall *et al.*, 2007). Performing a sensitivity analysis allowed me to test the relative impact of changing climate conditions within the range predicted by the AOGCMs.

I selected 10 AOGCMs, all shown by Milly *et al.* (2005) to be good predictors of contemporary precipitation

and runoff. The 10 AOGCMs used to define potential change in monthly precipitation values are shown in Table 1. These models are available on the Program for Climate Model Diagnosis and Intercomparison (PCMDI, 2007) and were compiled as part of the Intergovernmental Panel on Climate Change (IPCC) fourth model assessment. The SRES A1B climate scenario was used in all cases. SRES A1B is a moderate scenario in which energy use continues to increase, but technological advances stabilize emissions, leading to a CO_2 concentration of 720 ppm by 2100 (approximately double current concentration) (Nakicenovic & Swart, 2000). This single scenario was chosen because it represents the 'middle of the road' of expected future conditions absent policies to restrain greenhouse gas emissions. More importantly, the variability among climate models for projected precipitation change is greater than the variability among scenarios for any single model. Hence, using a single scenario, but a range of AOGCMs, provided a plausible range of potential future precipitation conditions in the western US.

Percent change in future monthly precipitation for each AOGCM was estimated by dividing average monthly precipitation modeled for 2090–2100 by average monthly precipitation modeled for 1971–2000. The 1971–2000 time period for current climate conditions was chosen to match the time period used in the PRISM average precipitation data. Projected monthly percent precipitation change for that 100-year time period was then averaged for the regions of grossly similar climate that cheatgrass could potentially invade: the state of California, the Intermountain West (NV, UT, ID, eastern OR, eastern WA), the Southwest (AZ, NM), and the Midwest/Colorado Plateau (CO, WY, MT, ND, SD, NE, KS). Percent precipitation change projections for the 10 AOGCMs were combined to determine the monthly maximum gain, maximum loss, and median percent change. Percent precipitation changes were applied by region to the PRISM dataset to simulate the range of possible future conditions. Temperature change was estimated by adding static increases of 2 and 4 °C to all of the western regions. In all cases the potential changes were applied to a single climate predictor variable at a time. This approach allowed me to test the relative sensitivity of potential cheatgrass distribution to each climate predictor variable individually.

Bioclimatic envelope modeling

Bioclimatic envelope modeling is a widely used method for defining suitable climatic conditions of a species based on the distribution of species occurrences. Numerous bioclimatic envelope modeling approaches have been presented and reviewed (Guisan & Zimmermann, 2000; Elith et al., 2006; Tsoar et al., 2007). For invasive species, approaches relying on presence-only data are more appropriate because absences do not always imply lack of climatic suitability. Presence-only data also make no assumptions about whether an area was sampled and the species not detected, or whether an area was not sampled. Absences may mean that the species has not yet invaded despite suitable conditions. Presence-only models include BIOCLIM (Busby, 1991), DOMAIN (Carpenter et al., 1993), HABITAT (Walker & Cocks, 1991), and Mahalanobis distance (e.g., Farber & Kadmon, 2003).

This study uses the Mahalanobis distance to predict climate suitability. Farber & Kadmon (2003) and Tsoar et al. (2007) recommend this approach for bioclimatic envelope modeling; it has been used to predict the ranges of rare species (Johnson & Gillingham, 2005; Rotenberry et al., 2006) and the potential ranges of invasive plants (Rouget et al., 2004). This modeling approach is a multivariate technique that defines perpendicular major and minor axes. Mahalanobis distances from a centroid in n-dimensional space are then calculated relative to the covariance of axes lengths. Hence, if the species is present within a narrow range of precipitation, but a wide range of temperature, equal Mahalanobis distances would cover a small range of precipitation, but a large range of temperatures. In two-variable space, an isoline defining equal Mahalanobis distance from the centroid is elliptical in shape, whereas equal Euclidean distance would be circular. A schematic example of Mahalanobis distances in two-variable space is shown in Fig. 2.

Table 1 Climate models used to assess projected change in precipitation by 2100

Climate model	Source
CCCma CGCM3.1	Canadian Centre for Climate Modelling and Analysis (Canada)
CNRM CM3	Centre National de Recherches Meteorologiques (France)
GFDL 2.1	Geophysical Fluid Dynamics Laboratory (USA)
GISS	Goddard Institute for Space Studies (USA)
HAD CM3	Hadley Centre for Climate Prediction (UK)
INM CM3	Institute for Numerical Mathematics (Russia)
IPSL CM4	Institut Pierre Simon Laplace (France)
MIROC 3.2	Model for Interdisciplinary Research on Climate (Japan)
MPI echam5	Max Planck Institute for Meteorology (Germany)
NCAR ccsm3	National Center for Atmospheric Research (USA)

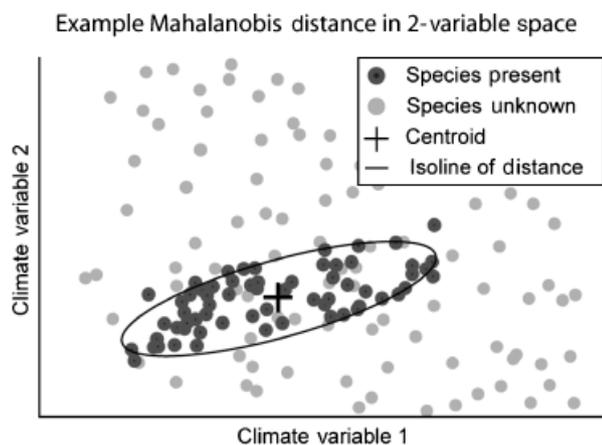## Example Mahalanobis distance in 2-variable space

Fig. 2 Schematic distribution of locations where species presence is known and locations where presence is unknown in two-variable climate space. The plus defines the centroid of the species presence points and the ellipse represents equal Mahalanobis distance capturing 95% of the presence points.

In order to identify the climate variables that best constrained cheatgrass distribution, I calculated the mean value of every PRISM climate variable (monthly mean temperature and precipitation) for all locations where cheatgrass is present (i.e., the sample mean). Calculating distance to the sample mean for every pixel in the sample and total populations gives an estimate of how constrained climate conditions are for the sample population relative to the total population. The difference between the median of the total and sample distances represents the extent to which the climate variable constrains the distribution of the species. A larger difference indicates a better predictor. This approach is similar in concept to the specialization factor presented by Hirzel et al. (2002). However, by comparing median values rather than standard deviations of sample and total populations, we reduce the influence of extreme values, which are frequently present when dealing with climate conditions in the western US. Resulting distances were normalized by the sample mean; hence, a normalized distance of 1 indicates that the median distance of the population is ± the sample mean.

The climate variables that best constrained cheatgrass distribution were selected by ranking the difference between median distance values for the total and sample populations. Once the best constrained predictor variables were identified, they were used to construct a bioclimatic envelope model for cheatgrass. For cases where predictor values had a high degree of correlation in the western US (e.g., June–September precipitation), I used the average of these variables to minimize redundancy. Seasonal averages rather than single months

were used because AOGCM seasonal projections were considered more robust. The number of variables used in the model was selected based on area under a receiver operating characteristic (ROC) curve, which plots the fraction of total pixels vs. the fraction of sample (invasive species) pixels that are within specific thresholds of Mahalanobis distances.

Area under the ROC curve increases as more cheatgrass presence points are predicted correctly relative to total points. Adding additional climate variables to the model improves the prediction, increasing the area under the curve. However, adding too many variables can over fit the data, resulting in a bioclimatic envelope model that is too constrained and produces an unreliable future range prediction. An optimal number of predictor variables can be identified based on area under the ROC curve because as more variables are added, the incremental improvement in the model decreases.

A map of climatic habitat for cheatgrass under current climate conditions was constructed based on the Mahalanobis distance. For comparison, Maximum entropy, or MAXENT (Phillips et al., 2006), a machine learning method that defines distributions based on simple functions related to each climate variable, was also used to project current cheatgrass climatic habitat based on the best climate predictor variables. The resulting Mahalanobis distances or MAXENT values that encompassed 95% of presence points were used to define climatic habitat. This methodological comparison was conducted to increase confidence in the use of Mahalanobis distance for describing cheatgrass' climatic habitat and assessing sensitivity to climate change.

To assess sensitivity to climate change, climate predictor variables were adjusted individually based on projected climate change scenarios from the AOGCMs. Mahalanobis distances for every pixel were recalculated using current climate conditions for the sample population and future climate conditions for the total population. The previously calculated Mahalanobis distance thresholds were used to assess suitability under climate change scenarios. Expansion and contraction of total land area within the 95% Mahalanobis distance threshold showed potential cheatgrass distributions with climate change.

Results

Modeling current suitability

The climate predictors that best determined cheatgrass distribution are the ones for which species presence is most constrained relative to the total study area. Sum-

Table 2 Best climate predictors of cheatgrass presence

Climate variable	Median normalized distance		Ratio of total/sample
	Sample population	Total population	
June ppt	0.67*	9.30†	13.93
July ppt	0.69	9.66	13.93
September ppt	0.65	9.02	13.90
August ppt	0.66	8.85	13.34
Average ppt	0.53	5.17	9.68
October ppt	0.59	5.35	8.99
May ppt	0.57	4.88	8.50
April ppt	0.58	4.14	7.08
January T_{max}	0.53	2.63	4.93
December T_{max}	0.55	2.51	4.54
February T_{max}	0.59	2.68	4.50
November T_{min}	0.61	2.63	4.35
December T_{min}	0.60	2.46	4.12

*Median distance value is $0.67 \times$ sample mean.
†Median distance value is $9.30 \times$ sample mean.

mer precipitation (June–September) variables are the best predictors of cheatgrass presence, followed by annual average precipitation, spring precipitation (April–May), winter maximum temperature (December–February), and winter minimum temperature (November–December) (Table 2). The worst predictors of cheatgrass presence were winter precipitation and summer maximum temperature. The distribution of June precipitation, which is the most constrained single variable and the best predictor of cheatgrass presence, for the sample and total populations is shown in Fig. 3. The distribution of July maximum temperature, which is the least constrained variable, is also shown for comparison.

Based on the ROC curve results, there was a substantial improvement from adding variables 1–3 (mean summer ppt, mean annual ppt, mean spring ppt), a small improvement from adding variables 4 and 5 (mean winter max temp, mean winter min temp), and minimal improvement from adding additional variables (Fig. 4). Thus, for cheatgrass, the bioclimatic envelope model is based on Mahalanobis distance calculated from the best five seasonal climate predictors.

Maps of climatic habitat based on Mahalanobis distance, and MAXENT are shown in Fig. 5. The spatial distribution of climatic habitat identified by Mahalanobis distance and MAXENT is similar. Under current climate conditions, the majority of cheatgrass climatic habitat under current climate conditions exists in northern Nevada, western Utah, southern Idaho, and eastern
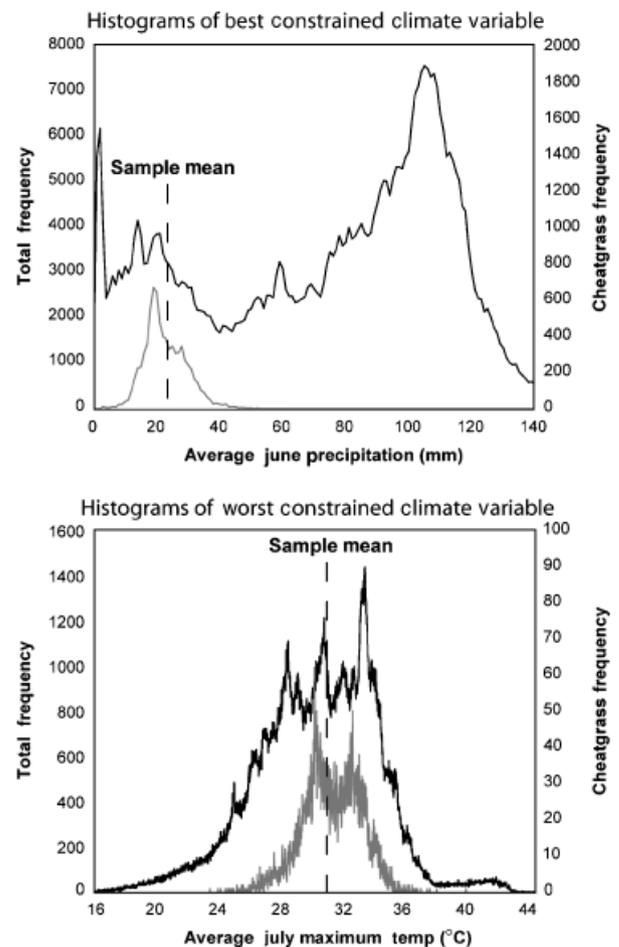

Fig. 3 Histograms of the best and worst constrained climate variables. (a) June precipitation is the best constrained variable. Cheatgrass (gray) distributions encompass a range of values much smaller than the total continental US (black). (b) July maximum temperature is the worst constrained variable. Cheatgrass (gray) distributions encompass a range of values almost as large as the total continental US (black). Dashed lines in both figures indicate the sample mean.

Oregon and Washington, all areas with extensive cheatgrass populations (Mack, 1981).

Predicting future suitability

Projected change in the western US varies considerably depending on the AOGCM selected (Fig. 6). For variables relevant to cheatgrass distribution, the AOGCMs consistently project a decrease in spring precipitation and an increase in annual precipitation, but changes in mean summer precipitation have a large range. In the Intermountain West for example, AOGCMs range from a projection of a 47% decrease to a 72% increase in summer precipitation. The maximum loss, median change, and maximum gain of precipitation for western
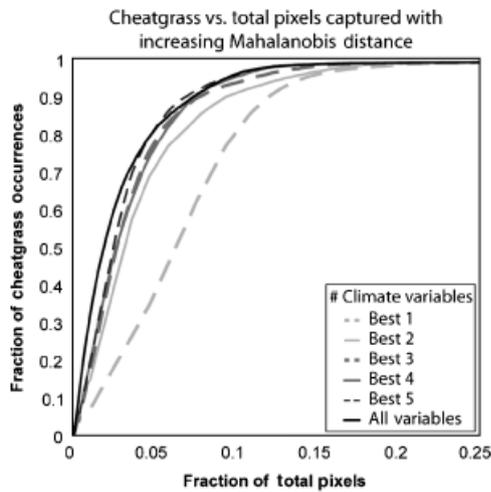
Cheatgrass vs. total pixels captured with increasing Mahalanobis distance

Fig. 4 Receiver operating characteristic (ROC) curves show the number of total pixels vs. cheatgrass occurrences mapped with increasing Mahalanobis distance as more climate variables are added to the model. The area under the ROC curve increases with the addition of up to five climate predictors. Additional climate predictors past the first five do not improve the prediction and may over-fit the model.

US regions based on the 10 AOGCM projections are shown in Table 3.

The total land area falling within Mahalanobis distances that capture 95% of the current extent of cheatgrass encompasses 760 000 km^2 of the western US. This value represents the maximum potential extent of areas at risk of ecosystem-altering cheatgrass invasion under current climate conditions. However, depending primarily on future precipitation conditions, suitable land area could increase by as much as 45% or decrease by as much as 70% by 2100 (Table 4).

The climate change scenario with the greatest expansion of climatic habitat is shown in Fig. 7. In this case, decreased summer precipitation opens vast areas of Montana, Utah, and Colorado to invasion. Valleys on the Idaho/Montana border and portions of southern Wyoming are most commonly at risk under the multiple scenarios tested.

Two scenarios in which climatic habitat contracts with climate change are shown in Fig. 8. Increasing summer precipitation (Fig. 8a) and increasing winter temperatures (Fig. 8b) lead to decreases in climatic habitat of 70% and 37%, respectively. Portions of southern Nevada and southern Utah are the most likely areas to become climatically unsuitable under the climate scenarios tested.

The median change case for all precipitation variables combined with a 2 °C increase in winter temperature is shown in Fig. 9. In this scenario, most of the currently suitable land area maintains suitability with climate
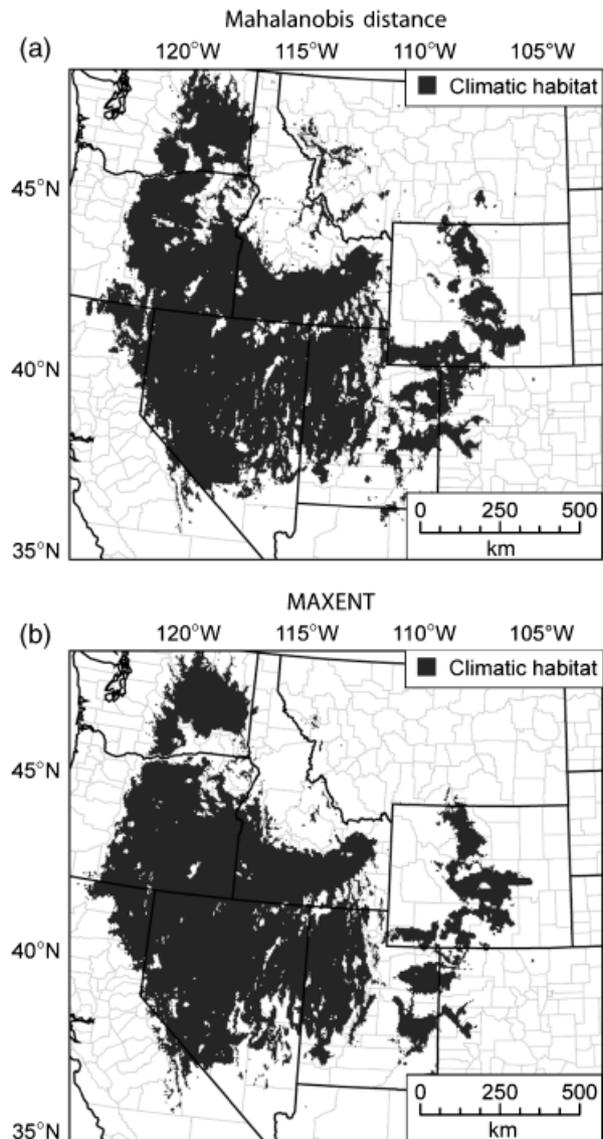

Fig. 5 Modeled climatic habitat for cheatgrass under current climate conditions. Gray areas correspond to (a) Mahalanobis distances and (b) MAXENT values that encompass 95% of mapped cheatgrass presence.

change. Parts of California and Wyoming lose their suitability to cheatgrass under this scenario, while other parts of Wyoming and Montana gain suitability.

Discussion

Expanding risk of invasive species as a result of climate change is a major concern for conservation and natural resource management (Dukes & Mooney, 1999; Moore, 2004). In the Intermountain West, invasive plants have been shown to expand quickly into new areas (Mack, 1981), and disturbance to native systems associated with climate change may further enhance invasion.
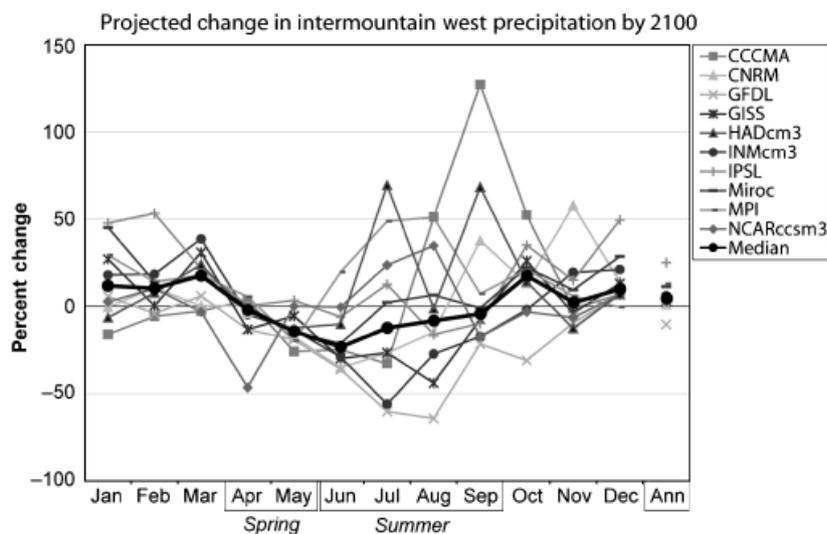
Fig. 6 Global climate model SRES A1B projections of change in monthly precipitation (%) for the Intermountain West by 2100. The median change of the 10 climate models shows a slight increase in fall/winter precipitation and a slight decrease in spring/summer precipitation.

Table 3 Projected changes of precipitation and temperature in cheatgrass relevant climate variables

Climate variable	Max decrease (%)	Median change (%)	Max increase (%)
California			
Spring precipitation	−59	−35	−1
Summer precipitation	−67	−10	+ 100
Annual precipitation	−21	−1	+ 37
Intermountain West			
Spring precipitation	−27	−6	+ 2
Summer precipitation	−47	−13	+ 72
Annual precipitation	−10	+ 4	+ 24
Southwest			
Spring precipitation	−67	−32	−4
Summer precipitation	−43	−12	+ 56
Annual precipitation	−21	−11	+ 20
Midwest/Colorado Plateau			
Spring precipitation	−8	+ 9	+ 30
Summer precipitation	−38	−12	+ 23
Annual precipitation	−8	+ 1	+ 20

Table 4 Change in suitable land area for cheatgrass for a range of 2100 climate projections

Climate variable	Change scenario	Suitable land area (km^2)	% Change
Current conditions	None	760 000	0
Summer precipitation	Max decrease	1 100 000*	+ 45
	Median change	860 000	+ 13
	Max increase	230 000†	−70
Annual precipitation	Max decrease	770 000	+ 1
	Median change	750 000	−1
	Max increase	660 000	−13
Spring precipitation	Max decrease	590 000	−22
	Median change	710 000	−7
	Max increase	720 000	−5
Winter temperature	2° increase	690 000	−9
	4° increase	480 000†	−37
Summer, annual, and spring precipitation	Median change	780 000‡	+ 3

Pixel sizes are calculated based on longitude length in kilometers at 40°N [longitude = cos(40) × 111 km] $n$pixels × 16.38 km^2.
*For geographic changes, see Fig. 7.
†For geographic changes, see Fig. 8.
‡For geographic changes, see Fig. 9.

Identifying land at risk, and the climate changes that might expand risk, can inform management decisions about prioritizing treatment of invasive plants.

The methodology applied here using the Mahalanobis distance is promising for modeling climate suitability for invasive plants (Rouget *et al.*, 2004). Mahalanobis distance compares favorably with other presence-only methods (Farber & Kadmon, 2003; Tsoar *et al.*, 2007), and produces a similar result to MAXENT (Phillips *et al.*, 2006) (Fig. 5), which also has high predictive accuracy (Elith *et al.*, 2006; Phillips & Dudik, 2008).

For cheatgrass, summer, annual, and spring precipitation variables are the best predictors of climate suitability (Table 2). The close relationship between cheatgrass distribution and narrow ranges of spring and summer precipitation (Fig. 4) values may be a

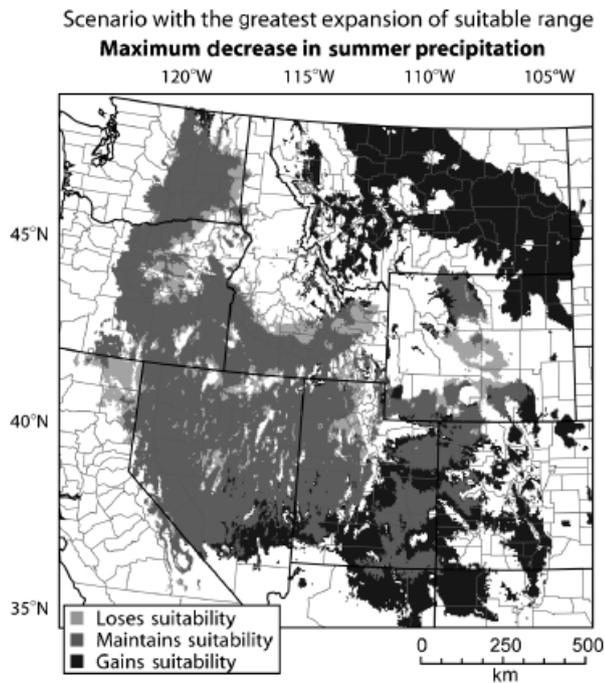Scenario with the greatest expansion of suitable range

Fig. 7 The maximum expansion of climatic habitat for cheatgrass occurs with a reduction of summer precipitation.

result of the different phenologies of cheatgrass and native shrub ecosystems that it commonly invades. With increased summer precipitation, native perennial shrubs and grasses may be more competitive because they are able to use water resources while cheatgrass is dormant (Loik, 2007). Where summer growing perennials are more competitive, cheatgrass is less likely to invade. Furthermore, increased summer precipitation may reduce the frequency of fire, one of the primary mechanisms of cheatgrass invasion. Similarly, a decrease in spring precipitation may reduce climatic habitat (Table 4) because cheatgrass does not have adequate water resources during its growing season.

In the scenario of maximum potential future expansion, decreased summer precipitation makes large portions of Montana, Wyoming, Utah, and Colorado climatically suitable for cheatgrass invasion (Fig. 7). Decreased summer precipitation may make perennials less viable and favor early season annuals such as cheatgrass. In scenarios of maximum potential future contraction, increased precipitation and/or higher winter temperatures lead to a loss of climate suitability in portions of Nevada, Utah, Idaho, Oregon, and Washington (Fig. 8).

The contrast between these best- and worst-case scenarios highlights how the uncertainty inherent in AOGCMs creates uncertainty in predictions of species distribution. AOGCM uncertainty is particularly problematic for precipitation change in the western US
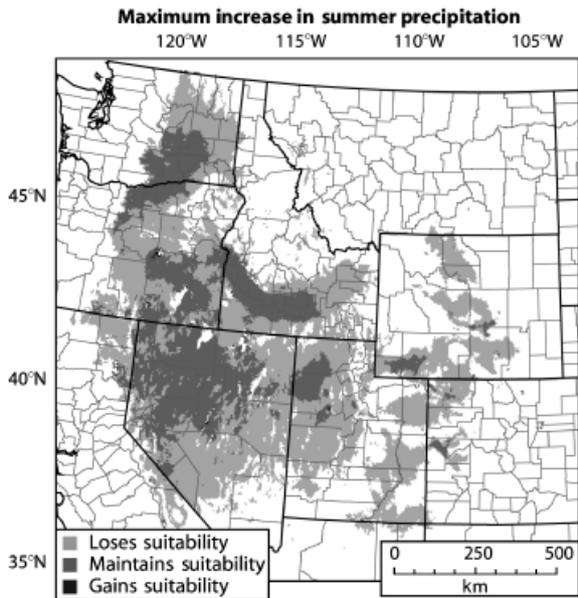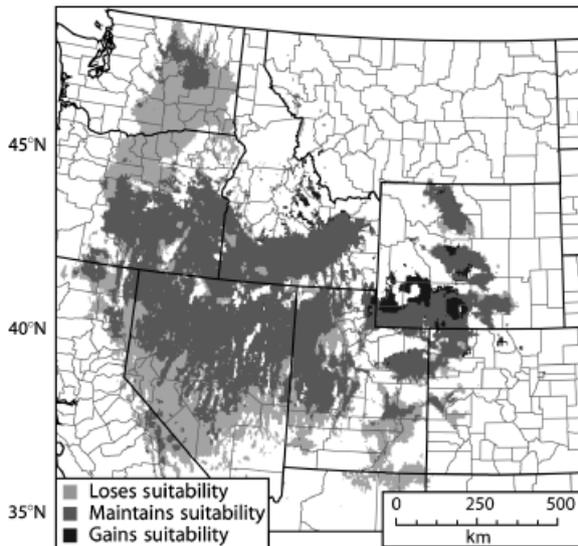

Fig. 8 Scenarios with maximum contraction of cheatgrass climatic habitat: (a) climatic habitat with maximum AOGCM projected increase in summer precipitation; (b) climatic habitat with a 4 °C winter temperature rise.

(Fig. 6; Table 3) due to complex topography and the difficulty of modeling El Niño (Randall et al., 2007). However, AOGCM uncertainty is likely a global problem and the range of predicted changes must be considered in species distribution modeling. Using any single global or regional climate model to predict change in climate suitability may lead to erroneous
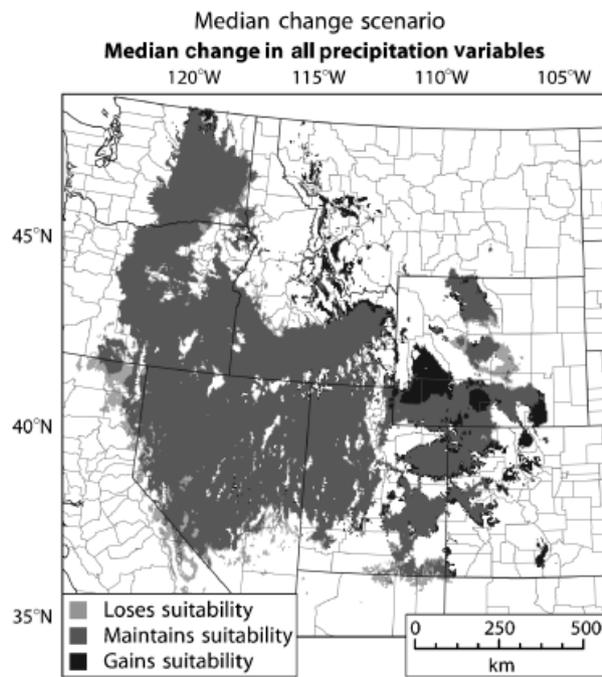
Median change scenario
Median change in all precipitation variables

Fig. 9 Cheatgrass climatic habitat under the median precipitation change scenario of 10 AOGCMs and a 2 °C winter temperature rise.

results and incorrect implications for management of invasive and/or native species.

The median climate change scenario has been used in efforts to identify the most likely future climate change, although this scenario does not represent conditions predicted by any individual AOGCM. This scenario results in an increase in cheatgrass climate suitability in southwest Wyoming and several valleys on the border of Idaho and Montana (Fig. 9). Although the land area impacted is smaller than the extreme climate change cases, this prediction is more moderate and should factor in management decisions for combating cheatgrass because it may be more likely to occur.

Despite the uncertainty in future climate conditions, the sensitivity analyses do show some consistency in risk and restoration potential. All future scenarios show some consistency of areas that maintain climate suitability (Figs 7–9). Cheatgrass populations remain consistently viable in parts of Nevada, along the Snake River plain in Idaho, in western Utah, and in eastern Oregon. Under most future climate conditions, these areas will continue to be at risk of cheatgrass invasion.

Only one scenario, reduced summer precipitation, results in a large expansion of climatic habitat (Table 4). Although this scenario represents an extreme case of climate change, reduced summer precipitation is projected by a majority of the tested AOGCMs. Furthermore, the extent of invasion potential makes this possibility important to consider in management plan-

ning in Montana and the Colorado Plateau (Fig. 7). Additionally, several areas are consistently at risk under multiple future climate scenarios, particularly parts of southern Wyoming and valleys on the Idaho/Montana border. Although the land area at risk in these cases is smaller than under reduced summer precipitation, the likelihood of occurrence is higher, making these areas high risk. Managers should be aware of these high-risk areas and treat small populations of cheatgrass.

Intriguingly, most of the climate change scenarios explored here result in a decrease in climatic habitat for cheatgrass (Table 4). The potential for contraction with climate change has also been predicted for other invasive species (Richardson *et al.*, 2000; Mika *et al.*, 2008). For cheatgrass, large portions of southern Nevada and southern Utah are most likely to become climatically unsuitable, either due to increased summer precipitation or higher temperatures. Under favorable climate change conditions, these areas are most likely to see reduced cheatgrass viability or competitiveness.

The bioclimatic envelope model presented here provides a first-order assessment of the geographic extents favorable to cheatgrass invasion under current and future climate scenarios. However, climate conditions only affect invasion at the broadest regional scale. Other factors relating to land use, soils, competition, or topography may affect the suitability of a given location. As a result, a hierarchical approach for assessing local-scale risk that includes a suite of environmental variables depending on the scale of the analysis has been recommended (Pearson & Dawson, 2003). For example, if the goal was to assess invasive species risk within a national park, we should first consider whether climate conditions are appropriate and then develop more specific risk relationships based on topography, land use, and soils (Larson *et al.*, 2001). In the case of cheatgrass, landscape-scale risk relationships with roads (Gelbard & Belnap, 2003) and other forms of land use, soils, and topography (Bradford & Lauenroth, 2006; Bradley & Mustard, 2006; Chambers *et al.*, 2007) have been established. A comprehensive evaluation of local-scale invasion risk should incorporate both regional risk from climate change and local risk from land use (Pearson & Dawson, 2003).

Potential changes to the distribution of cheatgrass' climatic habitat vary considerably depending on the AOGCM projection used. However, by empirically identifying the most constrained climate variable predictors and evaluating potential invasive distributions as those climate variables change, we can identify risk and restoration potential. Land managers should be aware that climate change will affect the potential geographic distributions of cheatgrass, and will likely affect other plant invaders as well. Managers of land at

risk under any of the future climate change scenarios can reduce risk by being increasingly vigilant in treating small cheatgrass infestations. These bioclimatic envelope model results emphasize the likelihood of large-scale changes in future distributions of invasive plants.

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