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Climate Change and Plant Invasions: Restoration Opportunities Ahead?

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Abstract

Rather than simply enhancing invasion risk, climate change may also reduce invasive plant competitiveness if conditions become climatically unsuitable. Using bioclimatic envelope modeling, we show that climate change could result in both range expansion and contraction for five widespread and dominant invasive plants in the western United States. Yellow starthistle (*Centaurea solstitialis*) and tamarisk (*Tamarix spp.*) are likely to expand with climate change. Cheatgrass (*Bromus tectorum*) and spotted knapweed (*Centaurea biebersteinii*) are likely to shift in range, leading to both expansion and contraction. Leafy spurge (*Euphorbia esula*) is likely to contract. The retreat of once-intractable invasive species could create restoration opportunities across millions of hectares. Identifying and establishing native or novel species in places where invasive species contract will pose a considerable challenge for ecologists and land managers. This challenge must be addressed before other undesirable species invade and eliminate restoration opportunities.

Introduction

Invasive plant species threaten native and managed ecosystems worldwide. They are increasingly expensive to control (Pimentel *et al.*, 2000) and have become a major component of global change (Vitousek *et al.*, 1996). Global climate change is expected to further expand the risk of plant invasion through ecosystem disturbance and enhanced competitiveness due to elevated CO_2 (Dukes & Mooney, 1999, Thuiller *et al.*, 2007, Weltzin *et al.*, 2003). However, climate change may also reduce invasive plant competitiveness if conditions become climatically unsuitable, creating opportunities for restoration in areas currently dominated by intractable invasive species. Although expanded risk from invasive plants due to climate change has been identified for several species (Beerling, 1993, Bradley, 2008, Kriticos *et al.*, 2003, Mika *et al.*, 2008, Sutherst, 1995, Thuiller *et al.*, 2007, Zavaleta & Royval, 2002), reduced risk from invasive plants due to climate change has received scant attention (Bradley, 2008, Mika *et al.*, 2008).

At global and regional scales, invasive plant distributions are limited by climate (e.g., Guisan & Zimmermann, 2000, Pearson & Dawson, 2003, Thuiller *et al.*, 2005). Bioclimatic envelope modeling is an approach for predicting potential species distributions based on the geographical relationship between occurrences and climate conditions. Although land use, soils, and species interactions are important for assessing invasion risk at local and landscape scales (Bradley & Mustard, 2006, Davis *et al.*, 1998), climate change is expected to lead to large-scale range shifts in species distribution (Hijmans & Graham, 2006, Hughes, 2000, Pearson & Dawson, 2003, Peterson *et al.*, 2002, Root *et al.*, 2003, Thomas *et al.*, 2004). Climatically suitable habitat, in either the present or future, can be defined as all areas with similar climate conditions to lands currently occupied by the target species (Fig. 1A). For invasive species, climate change can create both expanded risk, when more land area becomes climatically suitable (Fig. 1B) and/or

reduced risk, when land area currently at risk becomes climatically unsuitable for certain plant invaders (Fig. 1C). In some areas, currently invaded lands may also become climatically unsuitable, creating potential retreat areas which may provide opportunities for ecological restoration (Fig. 1C).

We assess the relationship between climate and species distribution for five prominent invasive plants in the western U.S.: cheatgrass (*Bromus tectorum*), spotted knapweed (*Centaurea biebersteinii;* Syn. *Centaurea maculosa*), yellow starthistle (*Centaurea solstitialis*), tamarisk (*Tamarix spp.*), and leafy spurge (*Euphorbia esula*). All of these species are defined as invasive because they originate outside of North America, they are able to dominate ecosystems, outcompete native species, and alter ecosystem function, and they are currently widespread and expanding in range. We then project range shifts due to climate change for each invasive species based on an ensemble of 10 atmosphere-ocean general circulation models (AOGCMs). Both expanded risk and restoration potential are likely for invasive species in the western United States.

Materials and Methods

We created bioclimatic envelope models based on the relationship between five invasive plant distributions and current climate conditions. Current plant distributions were based on regional maps of invaded distribution derived from remote sensing, or state and regional survey of weed managers. Using the invaded distribution to develop climatic envelopes is appropriate for invasive species because native and invaded distributions often encompass separate and distinct climatic envelopes (Broennimann *et al.*, 2007). Hence, using the native distribution to

predict invasion could be misleading because climatic and competitive conditions in the native range were not conducive to large-scale invasion.

Regional presence of *B. tectorum* relied on a 1 km spatial resolution map produced for the Great Basin using remote sensing, which identified *B. tectorum* based on its unique inter-annual response to El Niño (Bradley & Mustard, 2005). Regional presence of *C. biebersteinii* was based on a survey of species presence within the state of Montana conducted by the Montana Department of Agriculture (NRIS, Accessed 2007).

Regional presence of *Tamarix*, *E. esula*, and *C. solstitialis* was based on surveys commissioned by the Western Weed Coordinating Committee (Thoene, 2002, WWCC, 2002). Surveys of county level weed managers with the Department of Agriculture were conducted to gather expert opinion of the acreage of each invasive species within ¼ USGS Quadrangles (~ 6 km pixel size) in each county. Surveys were transformed into presence maps for each species using a threshold of 4 ha of species presence (>0.1% cover) within each pixel.

Presence data for the 5 invasive plant species were resampled based on nearest neighbor to a 0.04166 DD resolution (~4.5 km pixel size). This resolution was selected to match the Parameter-elevation Regressions on Independent Slopes Method (PRISM) interpolation of current climate data (Daly *et al.*, 2002). The PRISM climate interpolation is derived from U.S. weather stations and takes into account topographic influences on precipitation and temperature. Currently available climate data include monthly and annual averages of precipitation and temperature for the 1970-2000 time period.

Prior to creating an envelope model, it is important to select climate variables that best predict species presence. The best climate predictors were selected by identifying the ones that most constrained species distribution. To determine this, we compared the standard deviation of

each climate variable within pixels where the species was present to the standard deviation of all pixels (Bradley, 2008, Hirzel *et al.*, 2002). Climate variables with the smallest standard deviations across pixels with species present relative to all pixels were considered the most constrained. In cases where the top predictor variables were adjacent months (e.g., June and July precipitation), the mean of the variables was used. Climate variables tested were monthly and annual average precipitation, minimum temperature, and maximum temperature based on the PRISM dataset (Daly *et al.*, 2002).

Bioclimatic envelopes for each invasive species were created based on the Mahalanobis distance (Farber & Kadmon, 2003, Tsoar *et al.*, 2007), which is a presence-only multivariate technique that defines perpendicular major and minor axes and calculates distance from a centroid relative to covariance of axes lengths. The resulting envelope is ellipsoidal in n-dimensional shape. A presence only model is most appropriate for invasive species modeling because absences are of uncertain accuracy, potentially indicating either unsuitable climate conditions or suitable climate conditions that have not yet been invaded. Each model was based on four climatic variables. In all cases, four variables were found to model species distribution equally well as all of the available climate variables (Bradley, 2008). Suitable climatic conditions (land at risk of invasion) were calculated based on the Mahalanobis distance that encompassed 95% of the current species distribution.

Future climate conditions were derived from an ensemble of 10 AOGCM projections of precipitation, minimum temperature, and maximum temperature change by 2100 using the SRESa1b scenario (Nakicenovic & Swart, 2000, PCMDI, 2007). The following AOGCMs were used in this study: CCCMA-CGCM3.1, CNRM-CM3, GFDL-CM2.1, GISS-AOM, INM-CM3, IPSL-CM4, MIROC3.2(hi-res), MPI-ECHAM5, NCAR-CCSM3, UKMO-HadCM3. Average

monthly and annual climate change for each of 10 AOGCMs was calculated by subtracting the average conditions from 1970-2000 from the average conditions from 2090-2100. Modeled climate change was added to the PRISM interpolation of 1970-2000 average monthly and annual climate conditions. Although the spatial resolution of the AOGCMs was much coarser, the finer resolution of the PRISM dataset creates a higher-resolution estimate of local variation due to latitudinal and topographic effects. This method was most practical for an ensemble approach because regional climate models and downscaled results are available for only a small subset of AOGCMs.

The bioclimatic envelopes derived from the species distribution and current climate variables were applied to future climate projections. The Mahalanobis distance that captured 95% of the current distribution was used to project potential future distribution. The projected invasive species distributions for each of the 10 AOGCMs were summed to create an ensemble map of invasion risk under future climate conditions.

Results

Centaurea solstitialis dominates California grasslands and has become a serious agricultural pest, particularly due to its use of water resources (DiTomaso, 2000, Pitcairn *et al.*, 2006). Our analysis indicates the distribution of *C. solstitialis* in the western United States is most constrained by summer precipitation, spring precipitation, winter minimum temperature, and spring minimum temperature. Climatically suitable habitat currently includes much of California, eastern Oregon, and parts of eastern Washington (Fig. 2A). Climate change is likely to expand invasion risk from *C. solstitialis* to include more of California and Nevada (Fig. 2B). *C. solstitialis* populations in California, Oregon and Washington have low potential for

restoration of invaded lands (Fig. 2C). Of the currently invaded lands, only 1% are no longer climatically suitable by 2100 in any of the 10 AOGCMs tested. We assumed that future climatic suitability in 50% of the AOGCMs tested indicates continued high risk of invasion. 88% of currently invaded lands maintained climatic suitability in 5 or more of the 10 AOGCMs (Table 1).

Tamarix is a shrubby tree that occurs primarily in riparian ecosystems in the western United States, where it displaces native plants and threatens scarce water resources (Zavaleta, 2000). Its distribution is poorly constrained by climatic conditions; however, the best predictors are fall precipitation, summer precipitation, spring precipitation, and winter precipitation. Temperature changes are unlikely to affect *Tamarix* distribution. Climatically suitable habitat currently at risk is widespread, encompassing most of the land area of the western United States (Fig. 3A). Climate change has little effect on risk of *Tamarix* invasion, with the majority of land areas remaining climatically suitable (Fig. 3B); however, actual invasion risk is likely limited to riparian corridors. Similar to *C. solstitialis*, there is little potential for restoration of invaded areas (Fig. 3C). Of the currently invaded lands, only 2% are no longer climatically suitable by 2100 in any of the 10 AOGCMs tested. The vast majority of currently invaded lands (91%) are projected to remain suitable in 5 or more of the 10 AOGCMs tested (Table 1).

Bromus tectorum is an invasive annual grass that dominates shrublands of the inter-mountain west, leading to increased fire frequency (D'Antonio & Vitousek, 1992). *B. tectorum* distribution in the Great Basin is most constrained by summer precipitation, annual precipitation, spring precipitation, and winter maximum temperature (Bradley, 2008). Climatically suitable habitat currently at risk of invasion includes the majority of rangelands in the inter-mountain west (Fig. 4A). Climate change is likely to shift climatically suitable *B. tectorum* habitat northwards,

leading to expanded risk in Idaho, Montana and Wyoming, but contracted risk in southern Nevada and Utah (Fig. 4B). Central Utah, southern and central Nevada, which currently harbor extensive land area of *B. tectorum*, do not remain climatically suitable in the majority of the AOGCMs tested, showing potential for restoration (Fig. 4C). Of the currently invaded lands in the Great Basin, 13% are no longer climatically suitable by 2100 in any of the 10 AOGCMs tested, and 21% are only climatically suitable in one of the 10 AOGCMs. These areas encompass 40,000 km^2 and have the greatest potential for retreat. Only 8% of invaded lands are highly likely to remain at risk, maintaining climatic suitability in 5 or more of the 10 AOGCMs tested (Table 1).

Centaurea biebersteinii (Syn. *Centaurea maculosa*) is a biennial forb that invades rangeland and forest of the western United States (DiTomaso, 2000). *C. biebersteinii* distributions in Montana are most constrained by summer precipitation, fall minimum temperature, winter maximum temperature, and summer minimum temperature. Climatically suitable habitat currently at risk includes the foothills of the Rocky Mountains and the Colorado Plateau (Fig. 5A). Climate change is likely to shift suitable *C. biebersteinii* habitat to higher elevations, leading to both expanded and contracted risk in parts of Montana, Wyoming, Utah, and Colorado (Fig. 5B). *C. biebersteinii* populations in eastern Montana and lower elevations in western Montana do not remain climatically suitable in the majority of the AOGCMs tested, showing potential for restoration (Fig. 5C). Of the currently invaded lands in Montana, 17% are no longer climatically suitable by 2100 in any of the 10 AOGCMs tested, and 22% are only climatically suitable in one of the 10 AOGCMs. These areas, and low elevation invasions in other states, have the greatest potential for retreat. None (0%) of invaded lands are highly likely to remain at risk, maintaining climatic suitability in 5 or more of the 10 AOGCMs tested (Table 1).

Euphorbia esula is an invasive perennial herb that dominates northern prairies (DiTomaso, 2000, Leistritz *et al.*, 2004). *E. esula* distribution in the western United States is most constrained by winter precipitation, fall minimum temperature, spring maximum temperature, and annual precipitation. Climatically suitable habitat currently includes the majority of northern states west of the Mississippi River and some rangeland west of the Rocky Mountains (Fig. 6A). Climate change is likely to reduce risk from *E. esula* in states such as Colorado, Nebraska, Iowa and Minnesota (Fig. 6B). However, it may expand risk into parts of Canada not included in this study. *E. esula* shows strong potential for restoration in Nebraska and parts of Oregon and Idaho (Fig. 6C). Of the currently invaded lands in the west, 18% are no longer climatically suitable by 2100 in any of the 10 AOGCMs tested, and 13% are only climatically suitable in one of the 10 AOGCMs. Land area with retreat potential encompasses 67,000 km^2. Only 19% of invaded lands are highly likely to remain at risk, maintaining climatic suitability in 5 or more of the 10 AOGCMs tested (Table 1).

Discussion

In every bioclimatic envelope model, a precipitation variable was the best predictor of invasive plant distributions in the western United States. This point is important for two reasons. First, projecting plant distribution change based on rising temperature alone may produce misleading results, particularly in water-limited ecoregions such as those found in the western United States. Second, AOGCM projections of precipitation change are highly inconsistent between models; hence, an ensemble approach, such as the one used here, may lead to more robust species distribution forecasts than any one AOGCM alone (Araujo & New, 2007).

Projections of species distribution change based only on temperature, or using a single AOGCM projection may be of limited value.

Our results suggest that considerable changes in invasive species distribution may result from climate change. We have identified regions of the country that may become prone to invasion by one or more of these plants in the next century, as well as invaded lands which may no longer be climatically suitable for invasive species. Just as native species are expected to shift in range and relative competitiveness with climate change (Hijmans & Graham, 2006, Hughes, 2000, Pearson & Dawson, 2003, Peterson *et al.*, 2002, Root *et al.*, 2003, Thomas *et al.*, 2004), the same should be expected of invasive species. Depending on the species, this will create both expanded invasion risk and substantial restoration opportunities.

For 2 of the 5 species, *C. solstitialis* and *Tamarix*, our models predict primarily expanded invasion risk with climate change (Figs. 2-3). Many areas at risk already contain small but not yet dominant populations of these invaders, creating the potential for rapid expansion in the face of climate change. Continued invasion of *C. solstitialis* and *Tamarix* are likely in climatically suitable areas. Heightened monitoring and removal of nascent populations (Moody & Mack, 1988) increasingly will be necessary in areas where invasion risk expands with climate change.

For 3 of the 5 species, *B. tectorum*, *C. biebersteinii*, and *E. esula*, our models predict both reduced invasion risk and significant range contractions (Figs. 4-6). Lands with reduced invasion risk are unlikely to be invaded by the modeled species in the future. However, they may remain at risk from other invasive species or become at risk from invasive species not included in this study. For example, red brome (*Bromus rubens*), a relative of *B. tectorum*, is likely to replace *B. tectorum* in parts of the southern Great Basin where climate conditions become unsuitable for *B. tectorum*. Climate change poses a substantial challenge to invasive

species monitoring and management strategies because of the likely geographical shifts of invasion risk. Long-term management planning could benefit from more spatially explicit projections of invasion risk under current and future climate conditions.

On currently invaded lands that will become climatically unsuitable, invasive species are likely to be less competitive, potentially leading to retreat associated with climate change. Modeling and experimental work is needed to assess whether native species could occupy these sites if the invasive species are reduced or eliminated by climate change. (Native plants present prior to the arrival of the invasive plants may be unable to reoccupy these sites as a result of climate change). What may be required in these areas is 'transformative' restoration, involving the introduction of species native to the larger ecoregion that may not have been present originally but which can maintain ecological integrity (Harris *et al.*, 2006). Integrated modeling and experimental work is needed to develop and test viable species assemblages and approaches for transformative restoration. In the absence of active management, new invasive species may quickly become established in areas where the old invasive species are less competitive.

We second recent calls for inter-disciplinary thinking in the fields of conservation and restoration ecology to address challenges and opportunities resulting from climate change (Harris *et al.*, 2006, Millar *et al.*, 2007). The restoration opportunities and perils associated with the retreat of currently-intractable invasive species are vast in the western United States. The uncertainties associated with these changes, as well as the unknown make-up of viable future vegetation communities, highlight a pressing need for integrated modeling, monitoring, and experimental work to better address the ecological consequences of climate change. Without timely human intervention, the window of restoration opportunity presented by climate change may quickly close.

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Table 1: Currently invaded land area with restoration potential under 2100 climate scenarios.

		Number of AOGCMs that project future climatic suitability	**Percent of Currently Invaded Area**				
			Tamarix spp	*Centaurea solstitialis*	*Bromus tectorum*	*Centaurea biebersteinii*	*Euphorbia esula*
Restoration Potential	High	0	2	1	13	17	18
		1	1	1	21	22	13
		2	2	2	30	35	16
		3	1	3	18	19	16
		4	3	5	10	7	18
	Low	≥5	91	88	8	0	19

Figure Legends

Fig. 1. Schematic representation of climate-change scenarios for invasive species, showing the frequency distributions of invasive species (black dots) and all land cover (black line) relative to a hypothetical climate variable. A. Under current conditions, risk from invasion (gray fill) can be defined as all lands climatically similar to lands occupied by the invasive species. B. The worst case scenario is one in which conditions shift to increase the land area climatically suitable for invasion. C. The best case scenario is one in which climate conditions shift to decrease land area climatically suitable for invasion, potentially leading to a retreat in some currently invaded areas.

Fig. 2. Climate change is likely to expand invasion risk of *Centaurea solstitialis*, creating minimal retreat potential. A. *C. solstitialis* dominated lands in the western United States and climatically suitable habitat based on Mahalanobis distance. B. Change in future invasion risk based on the number of AOGCMs that project maintained climatic suitability. Colors represent risk of invasion based on the number of AOGCMs that project climatic suitability; black lines denote regions of expanded risk. C. Retreat potential of currently invaded lands. Note that most areas currently suitable for *C. solstitialis* maintain their climatic suitability in 5 or more of the 10 AOGCMs tested.

Fig. 3. Climate change is unlikely to affect the potential distribution of *Tamarix spp*. A. *Tamarix* dominated lands in the western United States and climatically viable habitat based on Mahalanobis distance. B. Change in future invasion risk based on the number of AOGCMs that project maintained climatic viability. Colors represent risk of invasion based on the number of AOGCMs the project climatic viability, hashed areas are expanded risk. C. Retreat potential of currently invaded lands. The majority of areas maintain climatic viability in 5 or more of the 10 AOGCMs tested.

Fig. 4. Climate change is likely to cause a shift in the range of *Bromus tectorum*, leading to both expanded and contracted risk as well as substantial retreat potential in southern Nevada and Utah. A. *Bromus tectorum* dominated lands in the Great Basin and climatically suitable habitat based on Mahalanobis distance. B. Change in future invasion risk based on the number of AOGCMs that project maintained climatic suitability. Colors represent risk of invasion based on the number of AOGCMs the project climatic suitability; lines indicate regions of expanded risk. C. Retreat potential of currently invaded lands. Note that dark blue areas maintain climatic suitability in 0 of the 10 AOGCMs tested.

Fig. 5. Climate change is likely to cause a shift in the range of *Centaurea biebersteinii*, leading to both expanded and contracted risk as well as substantial retreat potential in eastern Montana. A. *C. biebersteinii* dominated lands in Montana and climatically viable habitat based on Mahalanobis distance. B. Change in future invasion risk based on the number of AOGCMs that project maintained climatic viability. Colors represent risk of invasion based on the number of AOGCMs the project climatic viability, hashed areas are expanded risk. C. Retreat potential of currently invaded lands. Note that dark blue areas maintain climatic viability in 0 of the 10 AOGCMs tested.

Fig. 6. Climate change is likely to reduce invasion risk of *Euphorbia esula*, creating substantial retreat potential in several western states. A. *E. esula* dominated lands in the western United States and climatically suitable habitat based on Mahalanobis distance. B. Change in future invasion risk based on the number of AOGCMs that project maintained climatic suitability. Colors represent risk of invasion based on the number of AOGCMs that project continued climatic suitability; lines (very little area) denote regions of expanded risk. C. Retreat potential of currently invaded lands. Note that dark blue areas maintain climatic suitability in 0 of the 10 AOGCMs tested.

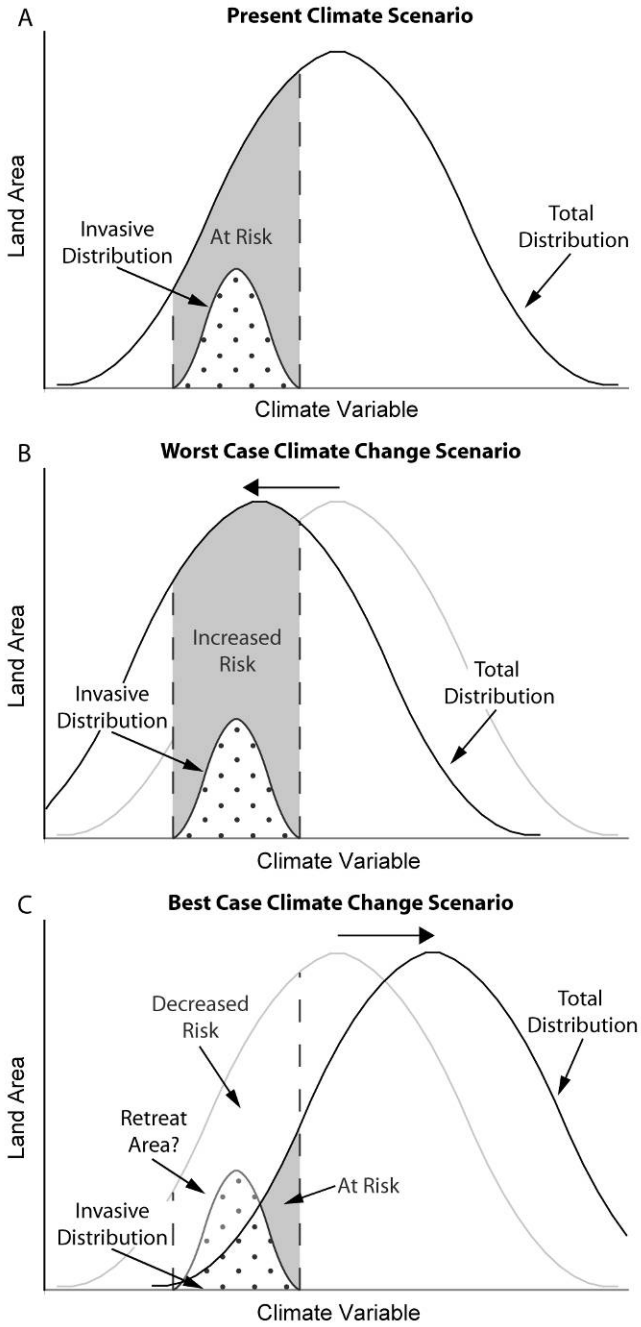
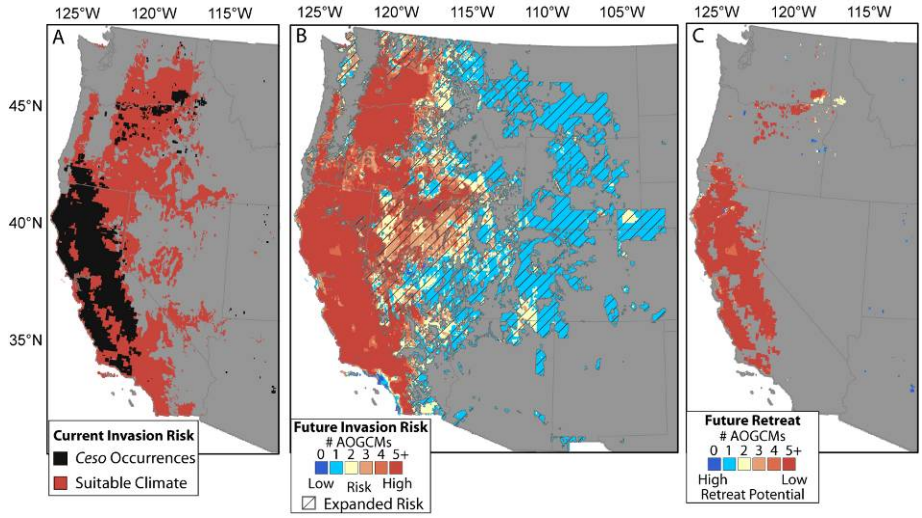

A
Present Climate Scenario
Land Area
Invasive Distribution
At Risk
Total Distribution
Climate Variable
B
Worst Case Climate Change Scenario
Land Area
Increased Risk
Invasive Distribution
Total Distribution
Climate Variable
C
Best Case Climate Change Scenario
Land Area
Decreased Risk
Total Distribution
Retreat Area?
At Risk
Invasive Distribution
Climate Variable

Figure 1


125°W
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Current Invasion Risk
Ceso Occurrences
Suitable Climate
Future Invasion Risk
AOGCMs
0 1 2 3 4 5+
Low
Risk
High
Expanded Risk
Future Retreat
AOGCMs
0 1 2 3 4 5+
High
Low
Retreat Potential

Figure 2

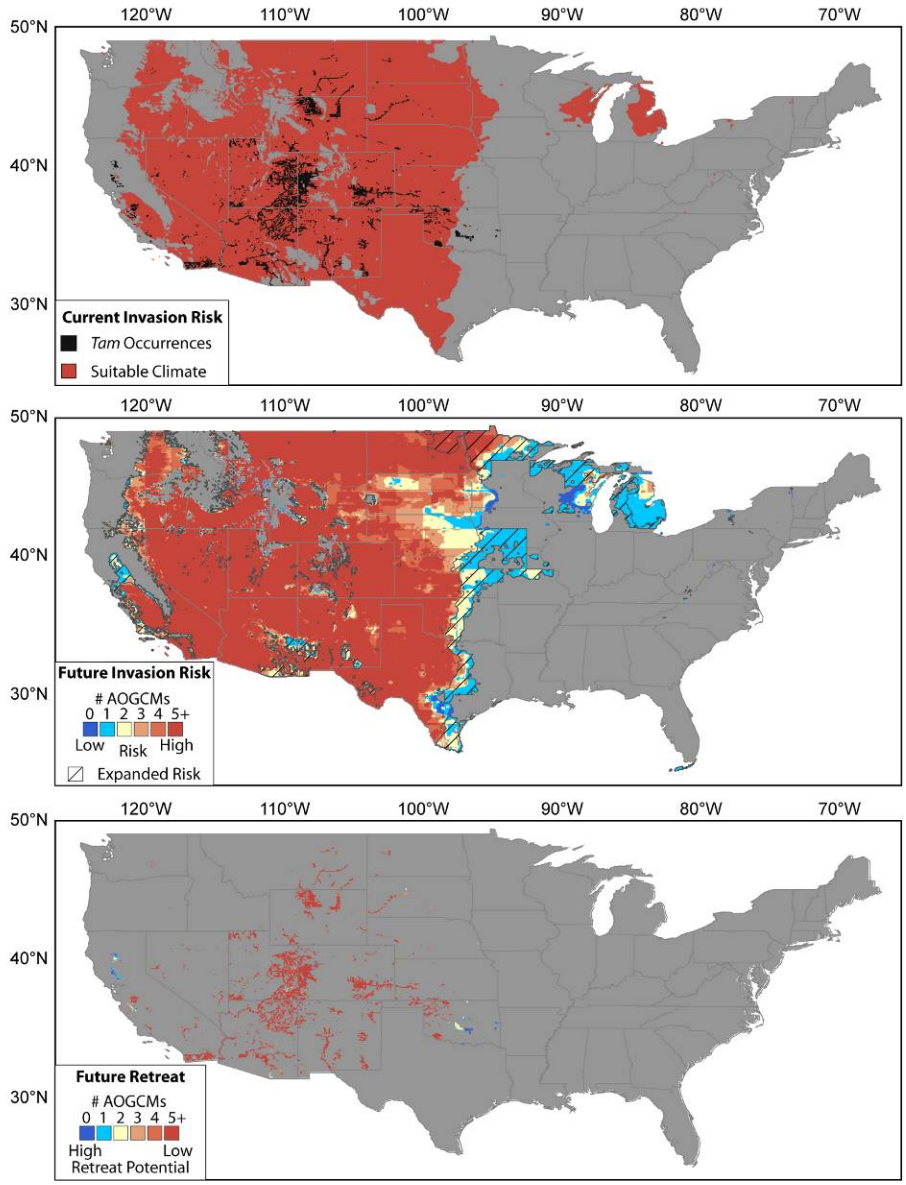
120°W
110°W
100°W
90°W
80°W
70°W
50°N
40°N
30°N
Current Invasion Risk
Tam Occurrences
Suitable Climate
Future Invasion Risk
AOGCMs
0 1 2 3 4 5+
Low
Risk
High
Expanded Risk
Future Retreat
AOGCMs
0 1 2 3 4 5+
High
Low
Retreat Potential

Figure 3

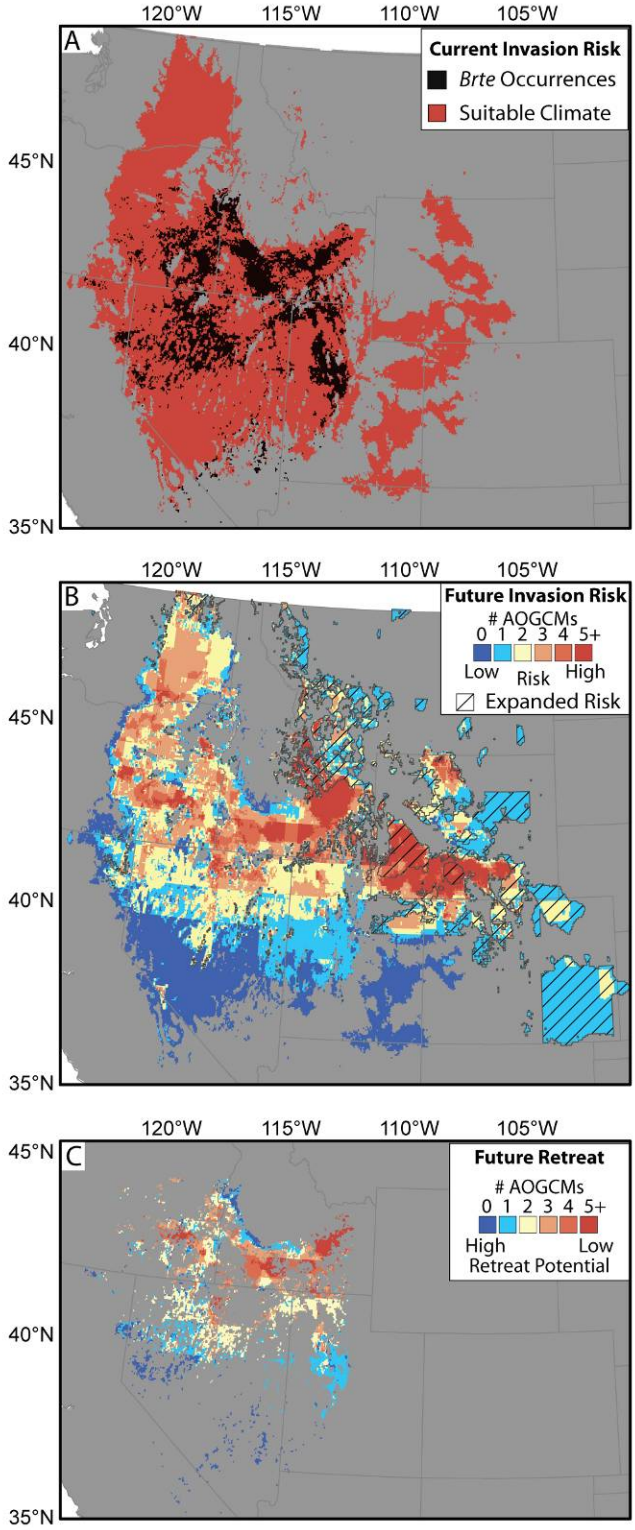
A
Current Invasion Risk
Brte Occurrences
Suitable Climate
B
Future Invasion Risk
AOGCMs
0 1 2 3 4 5+
Low Risk High
Expanded Risk
C
Future Retreat
AOGCMs
0 1 2 3 4 5+
High Low
Retreat Potential
120°W
115°W
110°W
105°W
45°N
40°N
35°N

Figure 4

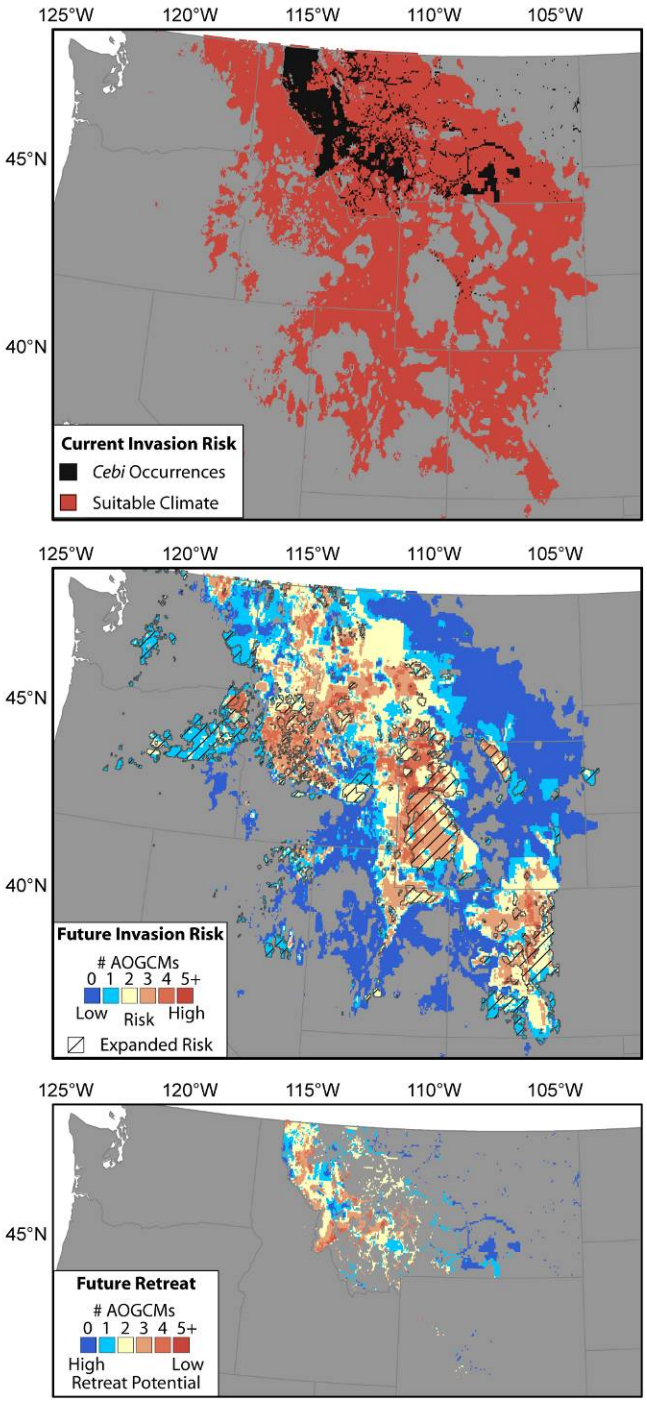
125°W
120°W
115°W
110°W
105°W
45°N
40°N
Current Invasion Risk
Cebi Occurrences
Suitable Climate
Future Invasion Risk
AOGCMs
0 1 2 3 4 5+
Low
Risk
High
Expanded Risk
Future Retreat
AOGCMs
0 1 2 3 4 5+
High
Low
Retreat Potential

Figure 5

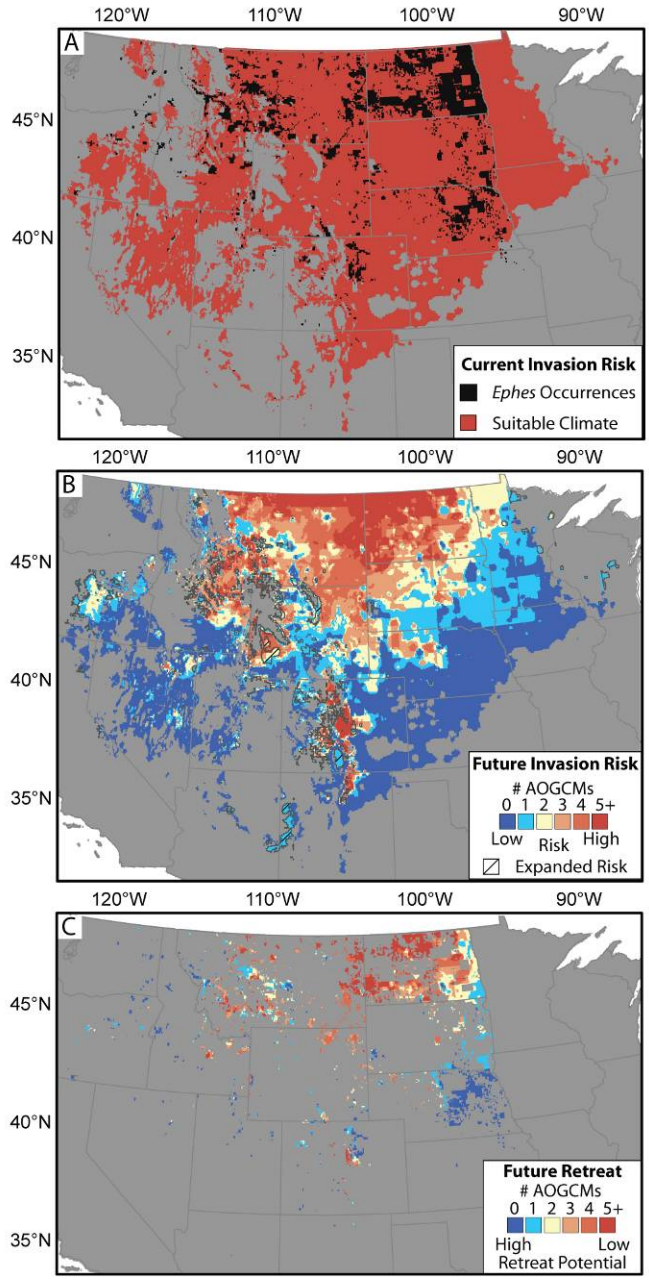
120°W
110°W
100°W
90°W
A
45°N
40°N
35°N
Current Invasion Risk
Ephes Occurrences
Suitable Climate
B
Future Invasion Risk
AOGCMs
0 1 2 3 4 5+
Low
Risk
High
Expanded Risk
C
Future Retreat
AOGCMs
0 1 2 3 4 5+
High
Low
Retreat Potential

Figure 6