Research

Modeling Tamarisk (*Tamarix* spp.) Habitat and Climate Change Effects in the Northwestern United States

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Tamarisk species are shrubs or small trees considered by some to be among the most aggressively invasive and potentially detrimental exotic plants in the United States. Although extensively studied in the southern and interior west, northwestern (Oregon, Washington, and Idaho) distribution and habitat information for tamarisk is either limited or lacking. We obtained distribution data for the northwest, developed a habitat suitability map, and projected changes in habitat due to climate change in a smaller case study area using downscaled climate data. Results show extensive populations of tamarisk east of the Cascade Mountains. Despite the perceived novelty of tamarisk in the region, naturalized populations were present by the 1920s. Major population centers are limited to the warmest and driest environments in the central Snake River Plain, Columbia Plateau, and Northern Basin and Range. Habitat suitability model results indicate that 21% of the region supports suitable tamarisk habitat. Less than 1% of these areas are occupied by tamarisk; the remainder is highly vulnerable to invasion. Although considerable uncertainty exists regarding future climate change, we project a 2- to 10-fold increase in highly suitable tamarisk habitat by the end of the century. Our habitat suitability maps can be used in "what if" exercises as part of planning, detection, restoration, management, and eradication purposes.

Nomenclature: Tamarisk, species in the genus *Tamarix* L., primarily *Tamarix chinensis* Lour. and *Tamarix ramosissima* Ledeb. and their hybrids.

Key words: Biomapper, climate envelope modeling, exotic plants, Ecological Niche Factor Analysis, saltcedar, species distribution model.

Species in the genus *Tamarix* are shrubs or small trees considered by some to be among the most aggressively invasive and potentially detrimental exotic plants in the United States (Stein and Flack 1996). Largely associated with the arid southwest and interior west, *Tamarix* spp. have been replacing native vegetation along rivers, streams, seeps, lakes, and reservoirs since their intentional introduction as ornamentals and windbreaks and for shade and erosion control in the 1800s (Pearce and Smith 2003). By the 1920s, these species were recognized as a serious problem in the southwest (DiTomaso 1998). *Tamarix* spp. are estimated to occupy approximately 650,000 ha (1.6 million acres) of primarily riparian floodplain habitat in 23 western states (Zavaleta 2000a). Although 8 to 12 species were introduced and have been found in the west, only about four species are highly invasive (Gaskin and Schaal 2002). The largest invasion consists of the morphologically similar *Tamarix chinensis* Lour. and *Tamarix ramosissima* Ledeb., with the most common plant in the U.S. invasion consisting of a hybrid between these two species that does not occur in their native ranges (Gaskin and Schaal 2002). We will refer to this complex of species and their hybrids simply as tamarisk in this paper.

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Interpretive Summary

Understanding invasive species distribution and habitat is critical for early detection and to coordinate management responses and eradicate species before they become widely established. It is also increasingly apparent that climate change has the potential to affect species habitat and distribution significantly. In this study, we spatially document the current distribution of tamarisk in Oregon, Washington, and Idaho and develop suitable habitat maps under historical and potential future conditions. Tamarisk species are shrubs or small trees considered by some to be among the most aggressively invasive and potentially detrimental exotic plants in the United States. Tamarisk is prevalent in the region, but major population centers are limited to the warm and dry environments found in the Northern Basin and Range, Columbia Plateau, and central Snake River Plain. Tamarisk is not a newcomer to the area; naturalized populations were reported as early as the 1920s. Although much of the region was mapped as low habitat suitability for tamarisk, sizable suitable unoccupied habitat prone to invasion exists. Large, relatively uninvaded areas of the region, such as the Columbia, Okanagon, Yakima, upper John Day, Deschutes, lower Salmon, upper Owyhee, and lower Snake Rivers and their tributaries, are vulnerable to infestation from small adjacent populations. Moreover, significant additional habitat could emerge by the end of the century because of climate change. There is uncertainty in projecting climate change effects, but considerable scientific consensus exists regarding future warming trends. Thus, it is likely that tamarisk habitat will expand in the northwest by the end of the century. Our results provide a useful starting point for discussing the emerging threat of this highly invasive species in relation to climate change.

Tamarisk has many attributes that can partially explain its successful invasion. Native to Eurasia, self-compatible and mature plants can produce over a half-million small, tufted seeds each year that can be carried long distances by wind or water (DiTomaso 1998; Gaskin and Schaal 2002; Sexton et al. 2002). Tamarisk also resprouts from roots and underground stems. Species in the genus are facultative phreatophytes that exhibit extensive root systems and are better able to tolerate lower ground water conditions, drought, water stress, and high salinity compared with the native species they often replace (Cleverly et al. 1997; DiTomaso 1998; Glen and Nagler 2005; Horton and Clarke 2001, Horton et al. 2001). The decline of many native riparian phreatophytes and the rise of tamarisk has been attributed to the development of water management programs that affect natural river flow regimes and change channel morphology and to stream diversions and ground water pumping for urban, agricultural, and industrial uses (DiTomaso 1998; Lite and Stromberg 2005; Shafroth et al. 1998).

Detrimental effects documented or proposed in association with tamarisk invasion are numerous and include decreased stream flow, excessive water use, loss of native biodiversity, effects on primary consumers and food web structure, salinization issues, and changes in channel morphology (Bailey et al. 2001; Birken and Cooper 2006; DiTomaso 1998; Kennedy et al. 2005; Ladenberger et al. 2006; Shafroth et al. 2005). Conservative economic estimates of mitigating these detrimental effects indicate that the annual costs of tamarisk to the western United States total US$280 to 450/ha (Zavaleta 2000b). The tamarisk problem is perceived as so serious that restoration is a major issue (Shafroth et al. 2008), and recent legislation specifically directed agency personnel to assess infestation extent in the western United States and demonstrate strategic solutions for management and reestablishment of native vegetation, among other activities (H.R. 2720: Salt Cedar and Russian Olive Control Demonstration Act). Some question the validity of certain claims of detrimental effects, and others point out benefits, including sediment stabilization and the creation of vertebrate habitat in riparian areas that can no longer support native vegetation (Cohn 2005; Glenn 2005; Lessica and DeLuca 2004; Owen et al. 2005; Pratt and Black 2006; Stromberg and Chew 2002).

Although tamarisk invasion has been studied extensively in the center of its distribution (Arizona, New Mexico, west Texas, Nevada, Utah, and southern California; Zavaleta 2000a) and, to a lesser extent, the northern plains (Sexton et al. 2006), we are aware of no studies in the published literature for the northwest (Oregon, Washington, and Idaho). Basic geographic distribution information, species–environment relationships, and potential habitat for the three-state region remain poorly understood and documented. In addition, typical descriptions of the current distribution for tamarisk frequently do not even include these states, although the species has been documented as far north as Montana in the interior United States (Lessica and Miles 2001; Pearce and Smith 2003; Sexton et al. 2006). For example, Bradley et al. (2009) document very limited populations in the three-state region. Morisette et al. (2006) report one presence point each for tamarisk in Oregon and Idaho, and none for Washington. Likewise, Friedman et al. (2005) report only one tamarisk point in eastern Oregon in the three-state region. Glenn and Nagler (2005) mention tamarisk presence along the Snake River in Idaho, but do not mention Oregon and Washington. We became increasingly aware through personal contact with local resource managers that tamarisk was not only present in the northwest, but was becoming dominant in some areas and of accelerating concern.

Our goals were to document the current distribution of tamarisk spatially in the northwest (Oregon, Washington, and Idaho) and develop potential suitable habitat maps under historical and future conditions with an Ecological Niche Factor Analysis (ENFA). Understanding species distribution and areas of suitable habitat on the basis of species–environment relationships is critical for early detection of developing invasions and to coordinate

Table 1. The extent, source, and type of data used to build a spatial tamarisk presence database.

Spatial extent	Source	Type/variable name and description
Washington, Oregon, Idaho	Colorado Department of Agriculture	Polygon shapefiles summarized by quarter quad
	T-Map (www.tamarixmap.org)	Point, line, and polygon shapefiles
	Herbaria	Electronic voucher records
	Invaders Database (http://invader.dbs.umt.edu)	Electronic location and infestation descriptions
Washington	Washington State Weed Coordinators	Point shapefiles, electronic location tables, paper maps
Oregon	Weedmapper (www.weedmapper.or)	Point shapefiles
NE Oregon	Tri-County Weed Management Area	Point shapefiles
Idaho	Idaho Department of Agriculture	Point and polygon shapefiles

responses for effective management and eradication of problem species before they become widely established. It is also increasingly apparent that climate change has the potential to significantly affect species habitat and distribution. Tamarisk has been projected to increase with future climate change and rising temperatures (Zavaleta and Royval 2001). To assess potential effects of climate change, we developed a climate-specific separate ENFA habitat model and then created maps for future habitat conditions (2070 to 2099) using climate data downscaled from two different climate model and emission scenario combinations that bracket a range of available future projections. We limited our examination of climate change effects and future habitat to a smaller case study area encompassing most of eastern Oregon and Washington.

Materials and Methods

Developing A Presence Database. To develop the presence database for tamarisk, we contacted state and local weed experts, examined herbarium data and online records, and created a single spatial layer of known tamarisk locations (Table 1). Data were imported into ArcGIS 9.2[1] from multiple sources and formats including point, line, and polygon information. Some data we obtained were reported as presence and abundance at the quarter quadrangle scale, and some data had to be digitized from hand-drawn maps or location descriptions (e.g., herbaria). All data formats were converted to points and combined into a single tamarisk presence dataset (n = 2,454). Line and polygon data were first converted to raster data and then resampled by establishing randomly selected 1-km–spaced points over the features. Lines were converted to points with XTools Pro,[2] and polygon data were converted with the use of a Hawth's Analysis Tool,[3] an automated random selection procedure (10% random selection). For polygons too small to use this procedure, one point was selected at the geometric center of the polygon.

Point data were then visually examined with 1-m (1 : 2,000) natural color aerial photography from the National Agriculture Imagery Program (NAIP 2004 to 2006) to assess data quality, evaluate point locations, and collect local condition information. Local condition information included a site description, adjacent site information, and riparian designation (Table 2). For points that were clearly not correctly located (e.g., a point in the middle of a reservoir, bare ground, or building or on a highway), the distance to a possible location was recorded by using the closest distance to any visible vegetation that could be tamarisk (mean ± SD, 15.2 ± 36.2 m; 50 ± 119 ft). However, we did not actually adjust the point locations. Each point was also assigned an error value based on the data source (141.1 ± 165.0 m). During this procedure, it was apparent that some sources had multiple

Table 2. Information on local condition and riparian status for tamarisk points. Local conditions were defined as the area immediately adjacent to the point using visual examination of 1 : 2,000 color air photos.

General description	%
Naturalized	81.2
Dirt/gravel road	4.6
Cultivated	4.0
Recreation/residential	3.8
Paved road	1.5
Irrigation ditch	1.0
Other[a]	5.8
Riparian designation	
Intermittent stream	51.4
Perennial stream	36.7
None/unknown[b]	10.9

[a] Each individual category in this group < 1% in descending order: dry lakebed, industrial, unknown, railroad line, urban, interstate/four-lane highway, quarry, reservoir.

[b] Category includes many extremely minor features such as pipeline, sewage treatment pond, etc.

points in a small area (e.g., a point for every tree), whereas other data sources only recorded a single point for an infestation with many trees. Thus, some areas were over- or underrepresented regarding the number of points compared with other areas.

On the basis of our assessment and findings above and partially to address sampling density bias, we converted the tamarisk point presence data to a 500-m cell grid. This resolution was also more consistent with the other spatial data used for modeling. Points west of the Cascade crest were eliminated because it was apparent that these were from plantings or residential locations. Ten points with large possible distances and data source errors (> 500 m) and 284 quarter quads were eliminated because we could not reliably convert these occurrences to a 500-m^2 grid. After these points were removed, and because multiple points could fall into a single 500-m grid cell, our final dataset for statistical summaries and modeling included a total of 1,044 tamarisk presence 500-m^2 cells. Local condition information (Table 2) is reported as the most common tamarisk point value within each grid cell. If ties were encountered (42 ties occurred out of the 1,044 cells, < 5%), local site condition values were selected randomly. For model development, the data were then partitioned into a training (90% or 940 cells) and model test dataset (10% or 104 cells). Cells were removed randomly from the dataset for testing after stratifying by ecoregion (minimum grid cells = 10 per ecoregion).

Habitat Modeling. Potential habitat under historical and future conditions was modeled with Biomapper 4.0.4.365,[4] which contains a suite of GIS and statistical tools designed to build habitat suitability models and maps. Biomapper is based on ENFA, which does not require absence data (Hirzel and Arlettaz 2003; Hirzel et al. 2002, 2004, 2006). We used this approach because of the difficulties in obtaining unbiased absence data (Hirzel et al. 2002). Bioclimatic envelope modeling approaches such as ENFA are based on the species distribution in environmental space and can be used to derive a map that represents the favorable areas for the species on the basis of current distribution and inferred environmental requirements. The approach is statistical and correlative and does not describe cause and effect between model parameters and response (Guisan and Zimmermann 2000; Hijmans and Graham 2006; Pearson and Dawson 2003), although we explored variables that are believed to be causal and driving forces for tamarisk presence and abundance and that coincide with physiological tolerances.

The Biomapper program computes habitat suitability functions by comparing the species distribution in the independent environmental variable space with that of the entire global environment (all map cells). In general, the distribution of the species of interest will differ from that of the whole set of cells with respect to its mean and standard deviation. These differences are used to define the species marginality (M, Equation 1) and specialization (S, Equation 2)

$$M = |m_G - m_S| / 1.96\sigma_G \quad [1]$$

$$S = \sigma_G / \sigma_S \quad [2]$$

where m is the mean, G stands for global, S stands for species, and σ is the standard deviation.

Application of these statistics to a set of variables leads to the concept of the ecological niche (Hirzel et al. 2002; Hutchison 1957). Marginality defines how particular the species habitat is relative to the global environment. Large values of M (close to one) indicate that the species lives in a very particular habitat relative to overall mean condition. Specialization relates to how restricted the habitat of the species is. Values exceeding one indicate that the species is restricted to the range of conditions that it can tolerate. Like Principal Component Analysis (PCA), ENFA summarizes all information into a few uncorrelated and standardized factors. But unlike PCA, these factors convey ecological information. The first factor, or axis, explains the species marginality, and other factors explain specialization. Habitat suitability (HS) is then calculated for each cell by assessing its location relative to the focal species distribution on all selected factors. Detailed presentation of the approach can be found in Hirzel et al. (2002).

We developed a set of nine ecogeographical variables (EGVs) based on important and potentially critically limiting factors as determined from the literature: 30-yr (1971 to 2000) annual means for: maximum and minimum daily air temperature, cumulative precipitation, degree days, frost days, total solar radiation, and solar duration. We also developed soil water storage and distance to water variables. Additional details are provided in Table 3.

Raster-based EGVs were resampled to a grid 500 by 500 m with the use of bilinear resampling in GIS (all climate- and DEM-based variables, Table 3). The vector-based distance to water variable (Table 3) was converted to a grid of 30 by 30 m, from which Euclidean distance was calculated and then resampled to 500 by 500 m, also by bilinear resampling. All EGVs were then converted to Idrisi-format raster layers and normalized by a Box–Cox transformation, and an ENFA analysis was completed. A HS map was produced using the number of retained significant factors from the ENFA according to the amount of variance explained and eigenvalue magnitude. For the HS algorithm, we used Veronika's with extreme optimum selected (Braunisch et al. 2008; A. H. Hirzel, personal communication). Other recommended algorithms (median, geometric; Hirzel et al. 2004) assume that the species density defines optimal habitat conditions. Because

Table 3. Independent variables explored for the habitat suitability models. All variables were converted to a grid cell size of 500 m^2.

Data type, source, and resolution	Variable name	Variable details
PRISM Gridded Climate Data,[a] 30-yr (1971–2000) annual means, 0.00833° (30 arcsec)	TMIN	Minimum daily surface air temperature
	TMAX	Maximum daily surface air temperature
	PPT	Cumulative precipitation
	DDAY[b]	Annual degree days: the absolute value of the 30-yr monthly mean minimum temperature multiplied by 30 and summed for the whole year (value exceeds 365 d)
	FROST[b]	Annual number of days below freezing: 30-yr monthly mean values ≤ 0 C were multiplied by 30 and summed
NRCS U.S. General Soils Map,[c] vector data[d]	AVLH20[b]	Available water storage at 1 m (cm^3)
DEM[e] and ArcGIS 9.2, 30 m^2	TSOLAR	Total solar radiation: calculated with ArcGIS 9.2 spatial analyst solar radiation tool
	DSOLAR[b]	Duration of solar radiation only: calculated with ArcGIS 9.2 spatial analyst solar radiation tool
National Hydrology High Resolution Dataset,[f] vector data[d]	H20DIST	Distance to nearest water (m): including perennial and intermittent streams, lakes, ponds, reservoirs, canals, etc.
CSIRO B1,[g] 30-yr (2070–2099) annual means, 0.00833° (30 arcsec)	TMIN_CB1	Minimum daily surface air temperature
	TMAX_CB1	Maximum daily surface air temperature
	PPT_CB1	Cumulative precipitation
MIROC A2,[g] 30-yr (2070–2099) annual means, 0.00833° (30 arcsec)	TMIN_MA2	Minimum daily surface air temperature
	TMAX_MA2	Maximum daily surface air temperature
	PPT_MA2	Cumulative precipitation

[a] PRISM Group, Oregon State University. http://www.prismclimate.org. Accessed May 22, 2007.

[b] These variables were dropped from the final models.

[c] Soil Survey Staff, Natural Resources Conservation Service, USDA. U.S. General Soil Map (STATSGO) for Oregon, Washington, and Idaho. http://soildatamart.nrcs.usda.gov. Accessed May 2007.

[d] Scale is not applicable for vector data (points, lines, polygons).

[e] Shuttle Radar Topography Mission (SRTM), USGS. Seamless SRTM "Finished" 1 arcsec (30-m posting) digital elevation raster. http://seamless.usgs.gov. Accessed July 18, 2007.

[f] USGS National Hydrography Dataset. http://nhd.usgs.gov. Accessed March 7, 2008.

[g] Data were downscaled from source data obtained from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel dataset (Meehl et al. 2007). http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php.

tamarisk in the northwest is at the edge of its current geographical range, we were worried that this assumption was not valid and that optimal habitat conditions might lie outside the observed environmental range, particularly for future climate conditions (Braunisch et al. 2008). The Veronika's with extreme algorithm relates the frequency of species presence to the availability of environmental conditions and evaluates species preference (Braunisch et al. 2008). Indeed, our original approach that used the geometric mean produced extremely counterintuitive results when the model was extrapolated to future climatic conditions.

We then conducted a 10-fold cross-validation process to both evaluate the predictive power of the model and reclassify the map. We report the continuous Boyce index ($B_{cont(w)}$, $w = 20$), which provides a summary of the model's prediction ability, and graphically present the cross-validation response curve, which provides several insights into model accuracy, including model robustness, resolution, and deviation from randomness (Hirzel et al. 2006). The cross-validation response curve was also used to reclassify the habitat map because continuous suitability (0 to 100) implies misleading precision (Hirzel et al. 2004, 2006). The cross-validation process allows one to define thresholds between suitable and unsuitable habitats, from which point the model does not add significant information, and calibrate the appropriate number and size of the habitat categories ("bins"). We adjusted thresholds by selecting the number and size of habitat categories that (1) minimized variance by choosing the maximum number of categories that were still statistically different from each other, (2) setting the lower HS threshold to 10 (appropriate for nonmobile species), and (3) linearizing the area-adjusted frequency curve (Hirzel et al. 2004, 2006).

In addition to this cross-validation, we also conducted two sensitivity analyses. These analyses allow us to asses under prediction; there is no feasible way to test overprediction. First, we used our 10% reserved test data to report the number of tamarisk presence test cells that fell within each of the HS classes. We also report this information by ecoregion, although not all ecoreigons had enough points (at least 10) for calculation. Misclassification rates are based on the number of cells that were classified as low suitability. We also used a set of 284 quarter quads that were omitted from the analysis and report the percentage of quarter quads that fell completely into areas that were mapped as low suitability. If any portion of the quarter quad coincided with the moderate- or high-suitability class cell, we considered those data correctly classified. Because of the spatial scale associated with these data (approximately 5,000 m^2) and the uncertainty surrounding how much tamarisk actually occurs within that large spatial extent, we did not analyze this information by ecoregion and suggest that these results be interpreted cautiously.

Climate Change Effects Modeling. To examine the HS of tamarisk under projected climate change, three key steps were required: (1) development of a climate-only habitat model for the entire study area with historical climate data, (2) development of downscaled future climate data for a smaller study area, and (3) extrapolation of the climate-only model developed in step 1 to the smaller study area by using the downscaled future climate data developed in step 2. For step 1, we developed a climate-only model for the whole study area in Biomapper using only historical climate EGVs: TMIN, TMAX, and PPT (Table 3). To model effects of climate change, nonclimatic effects on species distributions must be eliminated (Pearson and Dawson 2003). Procedures were as described above for habitat modeling, except that variables were not transformed because the untransformed model performed better than the transformed model, as assessed by explained information in Biomapper.

For the second step, future climate EGVs were developed with the use of climate data from two Atmosphere–Ocean General Circulation (AOGCM) and emission scenario combinations that essentially bracket some potential uncertainty in future climate projections: CSIRO-MK3.0/B1 and MIROC3.2(medres)/A2. The CSIRO model has a low temperature sensitivity, and the B1 emission scenario has atmospheric CO_2 stabilizing at around 550 ppm in 2100 (IPCC 2000). The MIROC model has a high temperature sensitivity and, when combined with the higher A2 emission scenario (atmospheric CO_2 is still increasing at around 850 ppm in 2100; IPCC 2000), provides a more extreme projection for future changes in climate.

Future climate data were downscaled from these two combinations with the use of interpolation methods similar to those described by VEMAP Members (1995). Average AOGCM climate anomalies between future and historical periods (2070 to 2099 and 1971 to 2000) were scaled to a 0.00833° grid (30 arcsec) by bilinear interpolation. The anomalies were applied to an observational historical grid derived from the PRISM model (Daly et al. 2007, 2008) to arrive at future fine-resolution (30-arcsec) values. We then generated 30-yr projected averages for the end of the century (2070 to 2099; Table 3). The 30-arcsec (~ 800-m^2) data were resampled to the final 500-m^2 grid by using bilinear resampling in GIS. Because downscaled climate data were only available for a subset of our project area (eastern Oregon and Washington), our projections are limited to this area.

We then developed future habitat maps (step 3) with the use of the new (future) climate EGVs from the smaller case study area and the Biomapper extrapolation program. The Biomapper extrapolation program essentially uses a climate-matching process. Habitat suitability values are generated for all combinations of factor classes from the historical climate–only model from the entire three-state study area (with the ranges extended 50% for the original factors) and saved in a "look-up table" file. Information is produced about the new future conditions on the basis of four different types of computations: (1) direct—a cell whose factor value combination existed in the original area in at least one cell, (2) interpolated—a cell whose factor value combination did not exist in the original area, but fell into the original range, (3) extrapolated—a cell whose factor values fell out of the original factor range, but is inside the margins set for extrapolation when building the model, and (4) not computed—a cell whose factor value combination was outside the margins of extrapolation and could not be assigned a habitat type. Confidence in output decreases from computation type 1 to type 4. Presentations of these cell types are informative in that one can see the extent of projected environmental change with the simulated new climatic conditions. Because we cannot cross-validate models that project events that have not yet occurred, these maps were placed into the low, moderate, and high habitat suitability categories using the same thresholds as defined for the present day climate model and map (A. H. Hirzel, personal communication).

Results and Discussion

Current Distribution. Populations of tamarisk species are prevalent in the northwestern United States, most notably east of the Cascade Mountains (Figure 1). Major population centers are limited to the warmest and driest environments found in the Northern Basin and Range (43% of presence grid cells), Columbia Plateau (33%), and

Figure 1. Tamarisk occurrence in the Pacific Northwest by Omernick's Level III Ecoregions (modified by splitting the North Cascades into east and west according to the Pacific Crest). This map shows all 2,454 tamarisk presence points, but only red points were included in our analysis. The yellow points were excluded from statistical and model analysis.

Table 4. Variance explained and Ecological Niche Factor Analysis (ENFA) score matrix for two analyses. Scores are listed by decreasing importance on factor 1.

	Factor 1	Factor 2	Factor 3	Factor 4
Full model				
Variance explained	45.5%	23.1%	21.9%	6.2%
Ecogeographical variables				
Maximum temperature (TMAX)	0.600	0.288	0.060	−0.786
Precipitation (PPT)	−0.467	0.871	0.207	−0.427
Minimum temperature (TMIN)	0.451	0.239	0.697	0.331
Solar radiation (TSOLAR)	−0.384	−0.319	0.683	−0.133
Distance to H_2O (H2ODIST)	−0.266	−0.012	0.031	0.272
Climate-only model				
Variance explained	69.7%	26.8%	3.5%	
Ecogeographical variables				
Maximum temperature (TMAX)	0.686	−0.450	0.714	
Minimum temperature (TMIN)	0.560	−0.175	−0.639	
Precipitation (PPT)	−0.465	−0.876	0.285	

central Snake River Plain (22%). All other ecoregions had < 2% tamarisk presence grid cells. The presence database used in this study does not represent a complete or randomized field survey, and data could be biased toward larger, accessible, and known populations of tamarisk. Given these limitations, we feel that our survey approach has most likely mapped major tamarisk infestations within the three-state region.

Overlaying our point data with color air photos indicated that these points were located in relatively naturalized sites (81%; Table 2). However, most (57%) points located in the relatively naturalized areas were adjacent to (within ~ 50 m) nonnaturalized, disturbed sites such as reservoirs (20%), roads and railroad lines (24%), and agricultural (6.2%) and recreational sites (4.0%). Visual examination of the color air photos also showed that most of the points were located near intermittent or perennial water sources (Table 2).

Interestingly, herbarium data indicate that tamarisk is not a newcomer to the northwest. Examination of 65 herbarium records from the region indicate the earliest tamarisk documentation was from a residential planting in Bingen, WA, in 1893 (Figure 1). Naturalized populations were reported by the 1920s, approximately the same time that tamarisk was recognized as a serious problem in the southwest. Yet until recently, perception in the northwest that tamarisk is a problem is not as pervasive as in the southwest, perhaps because water supply issues are not as critical in the northwest or from simply a lack of awareness. Or it might have been assumed that because many species were from warm, dry southern Eurasian climates, tamarisk populations would not survive or expand in colder areas (Sexton et al. 2002). Yet Baum (1978) noted that both *T. ramosissima* and *T. chinensis* originated in the cold, dry deserts of eastern Turkey and Korea, where winters can be severe and frost-free seasons range from only 60 to 120 d. Moreover, tamarisk species and their hybrids demonstrate a suite of evolutionarily labile traits. Sexton et al. (2002) proposed that plasticity and genetic diversity might allow tamarisk to invade colder climates in North America and colonize across extensive habitat gradients. The northern invasion of tamarisk might also have been facilitated by the existence of a novel U.S. hybrid of tamarisk (Gaskin and Schaal 2002), which has apparently introduced the genetic variability necessary for rapid (< 150 y) changes in the latitudinal gradient in cold hardiness (Freidman et al. 2007).

Habitat Suitability Model. We developed the final HS model and map with the use of only five independent variables: TMIN, TMAX, PPT, TSOLAR, and H2ODIST (Table 3). Initial model runs that used all nine variables indicated that minimum temperature, degree days, and frost days were all highly correlated (> 0.90) but that minimum temperature had more explanatory power. Available water storage contributed virtually no information to the model, although we suspect this is because of the nature of this data layer rather than a true lack of importance of the variable. We retained four out of the five factors, which explain 97% of the marginality and specialization (Table 4). The marginality factor alone accounted for 46% of the total variance. The training dataset provided an overall marginality of $M = 1.3$ and specialization value of $S = 2.1$. These values indicate that habitat for tamarisk is drastically different from the mean condition in the region examined and that the species is restricted in terms of range of suitable habitat conditions. Factor 1 coefficients show that tamarisk is positively

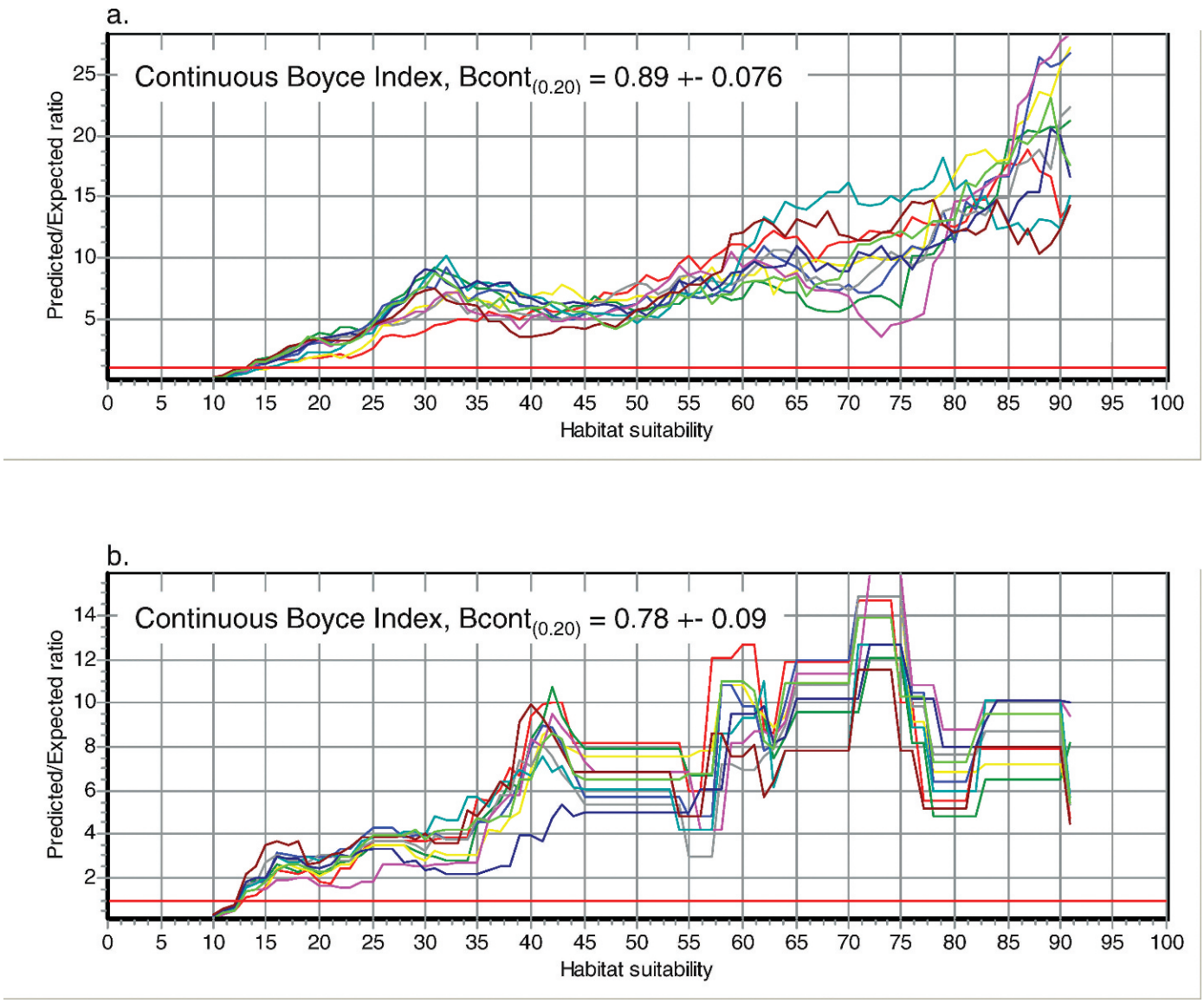

Figure 2. Cross-validation response curves and continuous Boyce indices ($Bcont_{(0.20)}$) for the full model (a) and the reduced climate-only model (b). Each colored line represents one of 10 cross-validation simulations. The red line (P/E = 1) defines where the predicted vs. expected (P/E) ratio equals 1, indicating that results are not significantly different than by chance.

associated with drier and warmer environments within the study area, with TMAX being the most important variable in the model. The next three factors account for more specialization. PPT, TMIN, and TMAX were particularly important. These results are similar to Friedman et al. (2005), who found that mean annual minimum and maximum temperature were strongly associated with tamarisk presence. In our HS model, the presence of tamarisk has a negative relationship with TSOLAR, which might simply reflect an elevational gradient. Distance to water (H2ODIST) was only marginally important, with tamarisk presence negatively correlated. Although the unimportance of this variable in the model is perplexing, given the species' association with riparian areas, it most likely reflects either issues with the data layer or that the climate variables have more explanatory power at this scale of analysis.

The continuous Boyce index from the cross-validation curve suggests the model is performing very well (Figure 2). Because the cross-validation process involved geographic partitioning, this performance is consistent across the study area. If the habitat suitability map were completely random, we would expect the predicted vs. expected (P/E) ratio to be 1 for all the habitat classes. Good models should have low ($P/E < 1$) and higher habitat suitability classes ($P/E > 1$) with a monotonic increase in between. The exponential shape of our response curve suggests that the model is not able to distinguish as many

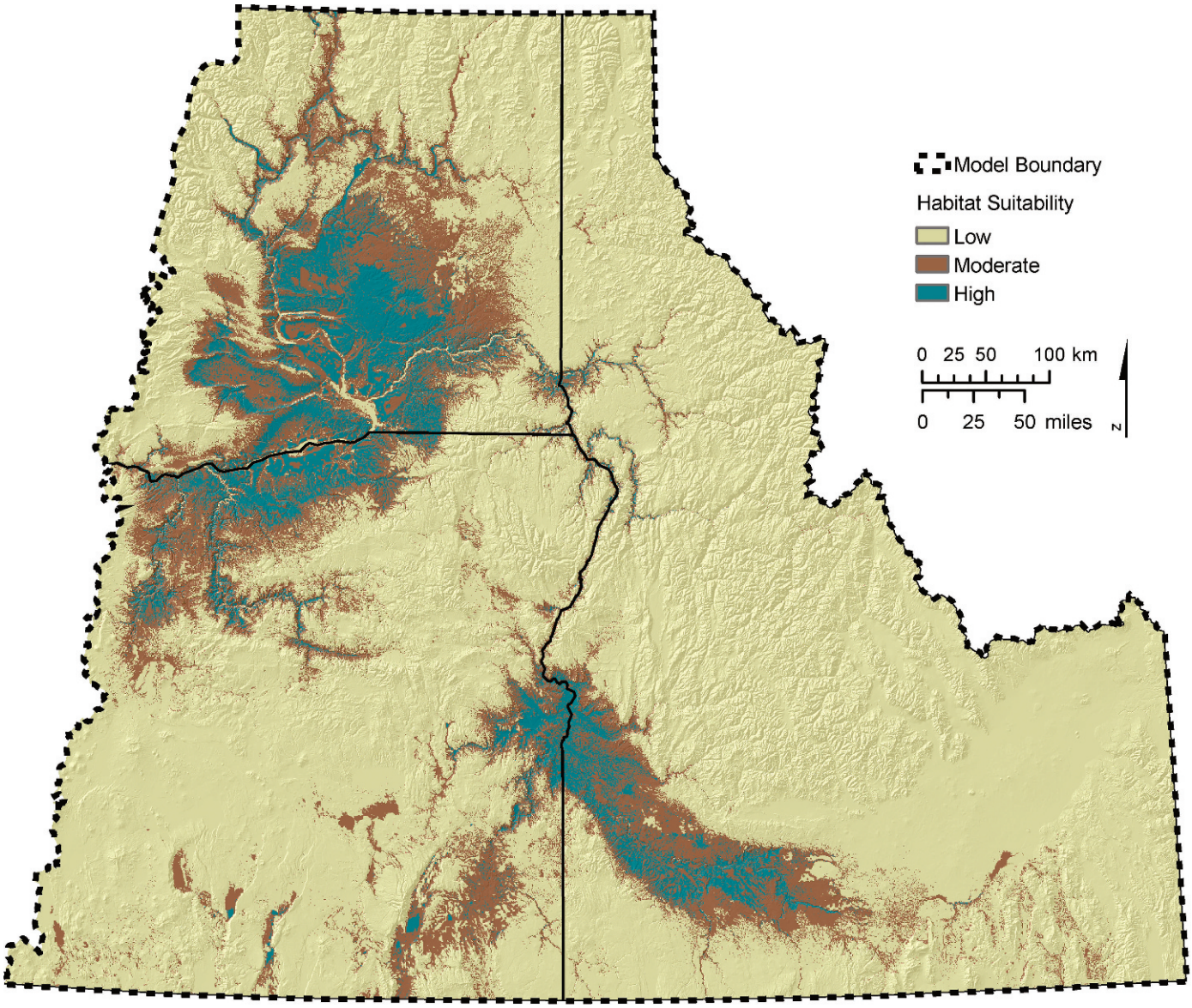

Figure 3. Habitat suitability (HS) for tamarisk as computed from a five-variable, four-factor ecological niche factor analysis.

different classes of suitability compared with a linear response curve, which has the highest resolution. However, linear response curves are rarely demonstrated (Hirzel et al. 2006). The variance across the cross-validation is narrow and widens as HS values increase, indicating that the model performs better in the low-suitability regions but is more variable about high suitability. The model also shows a maximum P/E ratio that greatly exceeds 1; thus, the model is able to differentiate species niche characteristics. It was apparent the model could not differentiate more than three habitat classes; thus, we reclassified the final map (Hirzel et al. 2004). We defined the HS threshold below 10 as low suitability and selected the boundary between moderate and high suitability (HS = 48) by examining the mean response curve and minimizing class variance. Details of the evaluation of the cross-validation response curve can be found in Hirzel et al. (2006).

Although much of the three-state region does not have suitable habitat (high and moderate classes) for tamarisk, sizable suitable habitat does exist (Figure 3). The majority (78.4%) of the region has a low HS rating for tamarisk, but 6.3% is classified as highly suitable habitat, and 15% as moderately suitable. However, $< 1\%$ of these suitable areas are currently known to be occupied by tamarisk.

Results from our sensitivity analysis with the 10% reserved test data reveal that our model did perform well. Only 6.7% of tamarisk presence cells were classified into unsuitable habitat (Table 5). Most cells were classified into either moderately or highly suitable habitat. Examination by ecoregion revealed that misclassification rates ranged

Table 5. Sensitivity analysis results of both the full and climate-only models and by Omernick's Level III Ecoregions.

	N	Habitat suitability class			% Misclassified[a]
		High	Mod	Low	
Full model					
10% Test data	104	49	48	7	6.7
Ecoregion[b]					
Northern Basin and Range	45	22	22	1	2.2
Columbia Plateau	34	14	15	5	15
Snake River Plain	23	12	10	1	4.4
Blue Mountains	2	1	1	0	0
Quarter quad data[c]	284	—	—	46	16
Climate-only model					
10% Test data	104	40	57	7	6.7
Ecoregion[b]					
Northern Basin and Range	45	29	11	5	11
Columbia Plateau	34	5	27	2	5.9
Snake River Plain	23	6	17	0	0
Blue Mountains	2	0	2	0	0
Quarter quad data[c]	284	—	—	98	36

[a] Based on the number of grid cells classified as low habitat suitability.

[b] Only ecoregions with at least 10 tamarisk grid cells are reported.

[c] Only those quarter quads that fell completely within the low suitability class are reported. Because of the spatial scale associated with the data ($\sim$ 5,000 m^2) and uncertainty surrounding how much tamarisk actually occurs within that large spatial extent, we did not analyze this information by ecoregion.

from 0 to 15%. The highest misclassification rate was associated with the Columbia Plateau, where we had ample training data that went into the model. We speculate that the higher misclassification rate in this ecoregion is actually due to fine-scale location issues associated with the data points. The sensitivity analysis conducted by using the quarter quads indicated a misclassification rate of 16%, which was similar to our highest ecoregion-specific misclassification rate. However, the higher misclassification rate for the quarter quads was largely due to misclassification in the southeast corner of Idaho. It is clear in Figure 1 that tamarisk is present and common in that area, but we lacked data at 500-m^2 scale to include in the model. Therefore this area was underrepresented in the model, and our map lacks suitable habitat for it. In addition, although we used a 500-m grid and dropped many data points, it is likely that observations are clustered, which could result in biases in ecological space and model misrepresentation of species ecological requirements. Despite these issues, our model generally fit the training dataset well, and our sensitivity analysis suggests that results are reasonable.

It is appropriate to use our HS map as (1) a general coarse-scale approximation of suitable habitat for tamarisk, (2) a means to select focus areas for further analysis, (3) a guide for tamarisk introduction and to monitor spread, and (4) a tool in planning effective restoration projects (Shafroth et al. 2008). For example, $< 1\%$ of the high and moderate habitat classes are occupied. Large areas of the region that are currently relatively uninvaded, such as the Columbia, Okanagon, Yakima, upper John Day, Deschutes, lower Salmon, upper Owyhee, and lower Snake (Hell's Canyon) Rivers and their tributaries, are vulnerable to infestation from adjacent and smaller existing populations. However, highly suitable areas currently unoccupied could remain so if concentrated early detection and mitigation efforts are deployed. We note that suitable habitat is only one factor when considering invasive species introduction and spread. Our study did not address other issues or include other potentially important variables such as sources or pathways of introduction, establishment and dispersal processes, genetic adaptation, hydrologic regime, fluvial and geomorphic processes, and biotic processes such as competition. Because of this, our maps most likely overestimate suitable habitat. For example, changes in natural river flow regimes and changed channel morphology are thought to be important factors related to the dominance of tamarisk along rivers and streams.

Climate Change Effects. Summary stats for the historical and future climate data show that by the end of century, both mean annual maximum and minimum air temperature could rise 1.7 to 5.0 C (Table 6). As expected, the

Table 6. Daily temperature (C) and precipitation (mm) summary statistics for the case study area for historical climate (PRISM) and two model/emission scenario combinations (CSIRO B1 and MIROC A2).

	Data source and time period		
	1971–2000	2070–2099	
Variable	PRISM	CSIRO B1	MIROC A2
Maximum temperature (TMAX)			
Mean ± SD	14.4 (2.5)	16.1 (2.5)	19.5 (2.6)
Range	2–20	4–21	7–25
Minimum temperature (TMIN)			
Mean ± SD	0.91 (2.2)	2.6 (2.2)	5.3 (2.23)
Range	−7–7	−6–8	−3–11
Precipitation (PPT)			
Mean ± SD	454 (303)	486 (324)	482 (352)
Range	160–3,060	170–3,300	169–3,500

MIROC A2 model and emission scenario combination produces the most dramatic changes in temperature. Both scenarios show an approximate 6 to 7% increase in precipitation annually.

Results from the climate-only HS model again are shown in Table 4. Factor 1 (marginality) alone accounted for almost 70% of the total variance. The dataset provided an overall marginality of $M = 0.99$ and specialization value of $S = 4.1$. The value of M close to 1 indicates that habitat for tamarisk is drastically different from the mean condition in the region examined. The large S value indicates that the species is very restricted in terms of range of suitable habitat conditions, which, in this case, is strictly related to climate. Again, factor coefficients show that tamarisk is positively associated with drier and warmer environments within the study area, with TMAX and PPT the most important variables in the model.

The continuous Boyce index from the cross-validation curve suggests the model performed well, but not as well as the full model (Figure 2). The habitat suitability model is not completely random and is able to differentiate species niche characteristics. Flat parts of the curve indicated that across the range of HS, the model cannot differentiate HS, and variance is very low. This is probably related to the low number of factors and variables in the model. As with the full model, variance increases as HS values increase. It was apparent the model could not differentiate more than three habitat classes; thus, we reclassified the final map (Figure 4). We defined the HS threshold below 10 as low suitability and selected the boundary between moderate and high suitability (HS = 66) by examining the mean response curve and minimizing class variance.

As with the full model, the climate-only HS map shows that most of the region has low habitat suitably for tamarisk (82% low suitability, 13% moderate, 5.1% high; Figure 4). Results from our sensitivity analysis that used the 10% reserved test data reveal that the climate-only model performed overall just as well as the full model, with only a 6.7% misclassification rate. Examination by ecoregion shows misclassification rates ranging from 0 to 11%. However, the sensitivity analysis conducted with quarter quads indicated a much higher misclassification rate of 36%. Again, the higher misclassification rate for the quarter quads was due in part to misclassification in the southeast corner of Idaho, and this area is not included in the climate change projections.

Future habitat maps for the case study area based on climate data for each model emission scenario combination are also shown in Figure 4, including the different types of computed cells that the Biomapper program produced. Both scenario combinations show significant additional habitat emerging in the study area in the future. The CSIRO B1 scenario projects that highly suitable habitat will increase from 5.2 to 12% by the end of the century, more than doubling. Moderately suitable habitat will increase from 19 to 30%. Most (89%) of the projected cells for this scenario have a direct analog to the EGV combinations that are based on historical climate data. This gives us greater confidence in the model projections. Only 9.3% of the cells represent novel conditions or new factor combinations (interpolated = 4.8%; extrapolated = 4.5%). A very small portion (0.96%) of the projected cells represent such novel conditions that the cells were not computed, despite the 50% extrapolation limit on the basis of historical climate conditions. For the MIROC A2 projection, the amount of highly suitable habitat increases dramatically to 51% by the end of the century, a 10-fold increase. Moderately suitable habitat increases from 19 to 34%. Because the MIROC A2 scenario is more extreme, it is not surprising that fewer (31%) cells have a direct analog

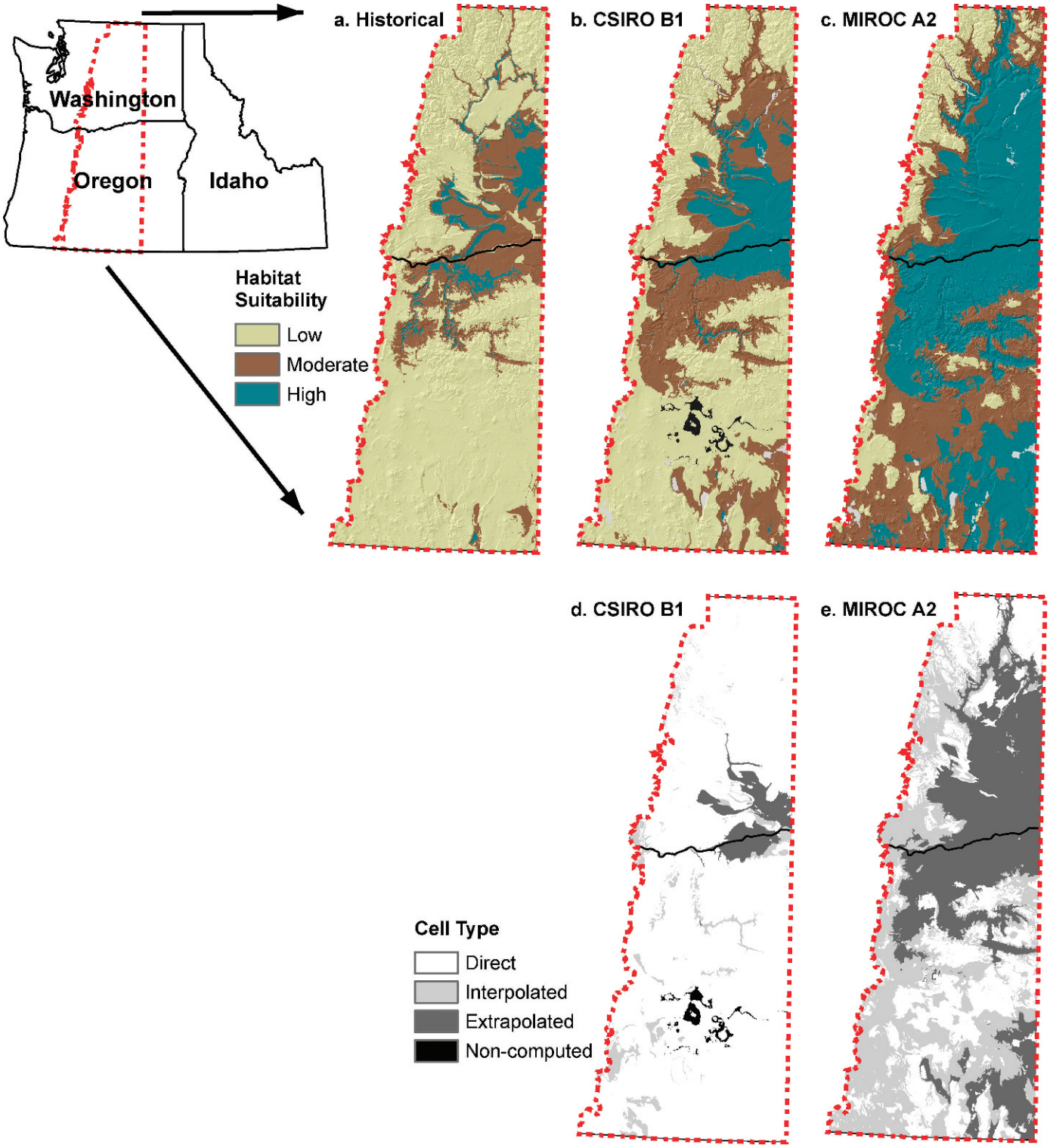

Figure 4. Projected changes in tamarisk habitat. (a) Historical (1971–2000) habitat suitability (HS) based on a climate-only model. Note that only the smaller case study area is shown in this figure, but the model was developed from the larger three-state region. (b, c) Future (2070–2099) HS under two model/emission scenario combinations: (b) CSIRO B1 and (c) MIROC A2. (d, e) Model-computed cell types.

to historical EGV combinations. The majority of cells were extrapolated (35%) and interpolated (34%). Interestingly, although the MIROC A2 scenario is considered a more extreme future, no cells were uncomputed for this projection.

Our future habitat maps provide useful "what if" examples for discussing the potential effect of climate change on tamarisk habitat. We caution that climate is only one factor in determining species habitat, and we stress that climate change projections should be examined within the context of multiple forms of uncertainty. Some of these issues have been discussed previously. Issues surrounding the nature of the climate system and climate model uncertainties should be acknowledged but are beyond the scope of this paper and can be extensively reviewed elsewhere (Bony et al. 2007; Roe and Baker 2007). Assessment of climate change effects is also confounded by our lack of knowledge about the future trajectory of greenhouse gas emissions. We attempt to address future greenhouse gas emission uncertainty by presenting two scenarios that bound some future emissions and model sensitivities to changes. Uncertainties related to the use of bioclimatic envelope models to examine potential changes in species habitat as a result of rapid climate change have been widely discussed in the literature (Davis et al. 1998; Guisan and Zimmermann 2000; Hampe 2004; Hijmans and Graham 2006; Martinez-Meyer 2005; Neilson et al. 2005; Pearson and Dawson 2003, 2004). One concern associated with climate change is that the potential direct effect of increased concentrations of atmospheric CO_2 on plant physiology and changes in water-use efficiency are not considered (Neilson et al. 2005; Pearson and Dawson 2004). However, because tamarisk is a phreatophyte, this latter point is less relevant (R. Neilson, personal communication, February 2008). Despite the uncertainties surrounding bioclimatic envelope models, the usefulness of the approach has been exemplified by recent prominent applications (e.g., Bradley et al. 2009; McKenney et al. 2007; Rehfeldt et al. 2006, 2008; Thomas et al. 2004).

Results from our case study area show that even for the more optimistic CSIRO B1 future model/scenario combination, highly suitable tamarisk habitat could expand more than twofold by the end of century because of climate change. As expected, the more extreme MIROC A2 combination shows much more habitat emerging. Indeed, a more than 10-fold increase in highly suitable habitat is projected, with most of the entire case study area outside of high-elevation regions becoming moderately and highly suitable. This outcome might seem far-reaching, but the projection makes sense given the MIROC A2 model/scenario combination and our largely temperature-driven ENFA and resultant HS model. We note that the MIROC A2 projections were largely based on interpolated and extrapolated cells; thus, we caution that confidence in this result is less robust. We were able to examine potential climate effects for just a portion of the study area, but it is likely that results for the entire region would be similar. Although there is uncertainty in projecting effects of climate change, there is considerable scientific consensus surrounding general future warming trends (IPCC 2007). Therefore, we suggest that it is likely that tamarisk habitat will expand in the northwest by the end of the century. Our potential future habitat maps provide a useful starting point for discussing the emerging threat of this highly invasive species in relation to climate change.

Sources of Materials

[1] ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA.

[2] XTools Pro, Data East, LLC, Moscow, Russia.

[3] Hawth's Analysis Tool, H. L. Beyer, http://www.spatialecology.com/htools.

[4] Biomapper 4.0.4.365, Alexandre H. Hirzel, University of Lausane, Switzerland, http://www2.unil.ch/biomapper/products.html.

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