Predictive Modeling of Cheatgrass Invasion Risk for the Lake Tahoe Basin

Final Report (revised Oct 31, 2010)

Includes nine figure (figure legends at bottom of report; figures included as separate documents). A GIS of cheatgrass suitability predictions is also associated with this report.

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Introduction

Cheatgrass (*Bromus tectorum*) is an exotic species of major concern that is increasingly detected in the Sierra Nevada. This notorious annual grass has been a major driver of ecosystem change in the intermountain west (Knapp 1996, Schwartz et al. 1996, Manley et al. 2000), due to its tendency to dramatically increase the frequency of early season fires via the highly flammable nature of its early-drying herbage (Brooks et al. 2004). While cheatgrass is present in some sites in the LTB, especially in drier, disturbed sites in the Carson Range, it is at a relatively early stage of invasion. Continued cheatgrass invasion and subsequent changes in fire regimes could result in increased frequencies of fire in forest and meadow habitats, loss of biodiversity and hydrologic function, and a lowering of habitat quality (Harris 1967, MacDonald et al. 1988, Hunter 1991, D'Antonio & Vitousek 1992, MacDonald et al. 1999). Cheatgrass invasion has fueled many recent, large and damaging fires on the Humboldt-Toiyabe National Forest just east and south of the Lake Tahoe Basin. There is at least some likelihood that extensive fuels treatment and forest and meadow restoration efforts in the Lake Tahoe Basin could facilitate cheatgrass invasion into meadows and open forest stands, possibly with serious consequences for forest and fire management (Keeley 2006). Just such a pattern has begun to occur on the western slope of the southern Sierra Nevada (Keeley and McGuiness 2007).

Climate change in the Sierra Nevada may also facilitate invasion by cheatgrass (Wagoner 1886, Hughes 1934, Ratliff 1985, Menke et al. 1996). Globally, the 1990s were the warmest of the last millennium (Mann et al. 1999), and 2006 was the warmest year on record (NOAA 2007). Earlier snowmelt is shrinking snowpacks, decreasing stream flows and ground water supply, and increasing drought stress on plants (Grabherr et al. 1994, McCarty 2001, Walther et al. 2002, Hamlet et al. 2005). Invasion by non-native species is an expected consequence of this anthropogenic change to Sierran habitats (Menke 1996, Schwartz et al. 1996, D'Antonio et al. 2004) and exotic plants are increasingly recorded throughout the Sierra Nevada (Manley et al. 2000). Montane meadows, which play important roles in hydrology, erosion control, nutrient cycling, provision of animal food and shelter, and human recreation (Kattelmann and Embury 1996), may be especially sensitive to climate change because of their high sensitivity to drying. Montane meadows have been suggested as early indicators of environmental changes associated with warming (Debinski et al. 2004). Global warming is likely to exacerbate the existing problem of meadow drying caused by overgrazing, ultimately leading to invasion by ruderal plant species like cheatgrass.

Here, we examine the relationship between climate and the invasion of cheatgrass. In an effort to forecast if climate change and disturbance will trigger further cheatgrass establishment and spread, we model the environmental factors related to current cheatgrass distribution and abundance in the LTB. Examining the distribution of cheatgrass along environmental gradients allows us to develop a spatially explicit predictive risk model of cheatgrass invasion and to apply it under both the current climate and future climate scenarios. In addition, we incorporate parameters for disturbance to improve model accuracy and predictive value. The resulting information will be useful for creating management scenarios to resist species invasion, restore natural communities, and sustain biodiversity and ecosystem function in the face of changing climate.

We assess three hypotheses:

H_1: Cheatgrass distribution is strongly related to gradients of precipitation, and cheatgrass is more prevalent at the drier end of the gradient, especially under high levels of disturbance (e.g., roads, urban areas).

H_2: Conditions suitable for cheatgrass establishment and spread are already widespread in the LTB, but the species has not yet reached most of these suitable locales.

H_3: Continued warming and summertime drying in the (projected) future will expand suitable habitat for cheatgrass establishment and spread in the LTB, which will be exacerbated by increased disturbance.

Methods

<u>Study system</u>

The Lake Tahoe Basin (LTB) in the Sierra Nevada of California and Nevada, United States, supports high topographic complexity and environmental variation. The total land area encompasses approximately 900 km^2 with elevations ranging between 1890 and 3317 m (a.s.l.). Mean winter and summer temperatures are -6 and 24° C, respectively. The majority of precipitation falls in the winter as snow and there is a strong decrease in precipitation from the west to east sides of the basin, with annual precipitation dropping from about 1500 mm to 500 mm. Cheatgrass (*Bromus tectorum*) is an exotic species of major concern in the LTB, and may prove to be the first exotic plant to become highly invasive and dramatically alter native-dominated communities within the basin. While it is increasingly detected in the basin, it is still at an early stage of invasion in comparison to lower elevation sites outside of the basin to the east.

<u>Species distribution models</u>

We applied four different species distribution models (SDMs) for testing our hypotheses that use different predictor variables and are calibrated at different spatial scales. To address our first hypothesis, we build a niche model using climate variables and surveys of cheatgrass from the LTB. This *local climate model* provides the best estimate of the realized climatic niche of cheatgrass within the LTB and shows which environmental variables are more important for constraining its local distribution. We also constructed a *local disturbance/dispersal model* using data from the LTB to test how non-climatic factors explain the distribution of cheatgrass within the LTB. For hypotheses 2 and 3 we build niche models calibrated with data from the distribution of cheatgrass throughout the northern hemisphere to get the best estimate of the species fundamental environmental tolerances. A *global model*, calibrated with climate data from the species native and invaded range throughout the northern hemisphere, is expected to provide the best estimate of the species' potentially suitable climate space both under current and future climate conditions. Finally, a *hierarchical (global + US) model* was used to test how climate and non-climate factors interact to constrain the distribution of cheatgrass. We expect that climate is a first order filter for determining suitable environmental space but that, especially in the invaded range, dispersal and disturbance factors may also be important mechanisms for determining the species distribution. The hierarchical model combined the estimate of the climate suitability from the global model and non-climatic factors from the species' invaded range within the United States as predictor variables. The climate niche is thus estimated using data from throughout the northern hemisphere while the dispersal/disturbance niche is estimated from data from the United States. Combining the data in one model allows for an estimation of the interactions between climate and non-climate factors.

Occurrence data

Occurrence data for calibrating the local climate and local disturbance/dispersal models and for validating all four models were collected using presence/absence surveys conducted between August and October of 2008 within the LTB. We surveyed 241 sites based on a stratified random sample of the existing environmental conditions that were accessible by either footpath trails or roads and were on public land. These criteria did not likely insert bias into our sampling methods because trails, roads, and public lands are extensive and well distributed across the LTB. Surveyed locations were recorded with a Trimble GeoExplorer XM 2005 global positioning system (GPS). Survey locations were differentially corrected and had an average positional accuracy of less than 3m.

For the global SDM and hierarchical model, occurrence data were downloaded from the Global Biodiversity Information Facility (http://data.gbif.org/; accessed July 17, 2008). Our goal was to acquire a more complete sampling of the total environmental conditions suitable to cheatgrass than represented in the LTB, providing a better reflection of its physiological tolerances. Thus, we acquired cheatgrass records for the entire northern hemisphere. Only the northern hemisphere was considered so that climate variables used in both distribution models corresponded to the same season. Only spatially unique records (one occurrence per grid cell) were used, totaling 7272 occurrence records and spanning 20 countries within North America, Europe and Northern Africa. Because the chosen modeling method requires both presence and absence data to run, we generated 10,000 randomly drawn terrestrial "background points" from within the same geographic extent as the occurrences and used these as "pseudo-absences" (Elith et al., 2006). Background points were restricted to countries in which occurrence points were available to limit the bias from unsampled regions.

Climate variables

Candidate environmental variables were selected based on a literature review of field and laboratory based studies and modeling studies (Bradley 2009, Sneva 1982, Young et al. 1969; Roundy et al. 2007, Evangelista et al. 2008). Bivariate scatter plots of climate variables from the global data set were visually inspected to screen-out variables that were highly correlated. If two variables were highly correlated, one of the variables was chosen to be included in the model based on its hypothesized importance for limiting the distribution of cheatgrass according to the reviewed literature. Additionally, variables were removed from the analysis if there was minimal variation in the variable across the LTB. The final selected predictor variables were mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation of the wettest quarter and precipitation of the driest quarter.

For the LTB, contemporary (late 20^{th} and early 21^{st} century) climate layers were derived by analyzing the difference between local meterological observations and modeled regional scale climate and then using statistical models to correlate these differences to physiographic features (Dobrowski et al., 2009). Climate layers for Lake Tahoe were resampled from 30m x 30m to a 200m x 200 m grid cell resolution. Global contemporary climate data were downloaded from the 30 arc-second (approximately 1km x 1km) monthly dataset on the WorldClim website (http://www.worldclim.org/; accessed July 8, 2009 (Hijmans et al., 2005)).

To derive future climate layers, we used projections from climate models from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset. The data were obtained from bias-corrected and spatially downscaled climate projections derived from CMIP3 data (http://gdo-dcp.ucllnl.org/downscaled_cmip3_projections/ described by Maurer et al. (2007)). We used data from the SRES A2 emission scenario. The A2 emission scenario represents a high end or "business as usual" scenario of moderate to high continued greenhouse gas emissions (IPCC, 2007) and observed climate over the last several years seems to be most closely matching this scemario. Future climate projections were summarized in 5-year intervals from 2015-2059.

Future climate projections were statistically downscaled to match the spatial resolution of the contemporary climate data using methods from Tabor and Williams (2010). Anomalies between modeled future climate and modeled 20th century climate were resampled to 200m x 200m resolution using bilinear interpolation. The downscaled anomalies were then added to the observed climate of the 20th century to obtain the projected future climate.

Disturbance/dispersal variables

Roads and urban areas are known to be important for aiding in the dispersal of invasive species and in causing disturbances that allow invasive species to establish (Gelbard and Belnap 2003, Von Der Lippe and Kowarik, 2006). We used the USGS major roads of the United States layer (http://nationalatlas.gov/mld/roadtrl.html; accessed 4/19/2010) to calculate a distance to roads throughout the United States. This layer includes interstate routes, state highways and other large roads. We calculated the distance from urban areas using the USGS urban areas of the United States layer (http://nationalatlas.gov/mld/urbanap.html; accessed 4/19/2010) which shows built-up areas within the United States where large human populations exist. Existing vegetation can inhibit the establishment of invasive species in new areas. The percent cover of herbaceous vegetation and trees for the United States was derived from MODIS satellite data (Global Land Cover Facility, www.landcover.org, accessed 4/19/2010). For the LTB, the cover of herbaceous vegetation and trees was derived from IKONOS satellite data (Greenberg et al., 2006). Extensive work has shown that fires allow cheatgrass to invade ecosystems and once established increase fire frequency (Brooks et al. 2004). We used the Wildland Fire Decision Support System's historical fire perimeters (2001 to 2008) data layer (http://frames.nbii.gov/documents/wfdss/Historical_Fire_Perimeters_Page.html; accessed 4/19/2010) to calculate the distance to fires within the United States and LTB.

Distribution models

Boosted regression trees (BRT) were used to model the relationship between climate and the occurrence datasets. BRTs are a nonparametric statistical algorithm that fit non-linear functions to the data and allows for efficient fitting of interactions without prior specification (Elith et al. 2008). BRT's have been shown to have superior predictive performance in comparisons with other algorithms using both presence/absence (Duncan et al. 2009) and presence-only data (Elith et al. 2006). All models were fit with the gbm (Generalized Boosted Regression Models) package (Ridgeway 2007) in R version 2.9.0

(R Development Core Team, 2009) with modifications provided by Elith et al. (2008). Models were fit with a tree complexity of 3(i.e., the number of nodes in each tree) and a learning rate of 0.01 (i.e., determines the contribution of each tree to the growing model), which always resulted in at least 1000 trees, a rule of thumb given by Elith et al. (2008). Model predictions from the global climate model and the hierarchical (global + US) model were projected to the LTB dataset and the local climate model and global climate model were projected to the simulated future climates. The output from the BRT models is a continuous surface between 0 and 1; these values can be projected across geographic space. For the local climate model, the predicted value at a cell can be interpreted as the probability of occurrence, or risk, of cheatgrass given the climate variables for the cell. However, because the global models are built with presence-only data, we have no knowledge of the true prevalence of the species and thus the interpretation of the predicted values is slightly different. The predicted value can be thought of as index of climatic suitability at that cell, with high values equal to greater suitability. Although the predictions from presence-only models are not directly comparable to the predictions from presence/absence models, we refer below to the predictions of both models as suitability scores, for simplicity.

The area under the receiving operator characteristic curve (AUC) was used as a threshold-independent assessment of model accuracy. The AUC varies from 0 to 1 with values of 1 meaning the model discriminates presence sites from absences perfectly, while values of 0.5 mean that presences are discriminated from absences no better than random and values less than 0.5 indicate predictions are worse than random. Additionally, predictions were converted to binary presence/absence predictions to assess omission (false negative; underprediction) errors and commission (false positive; overprediction) errors. The threshold used to convert continuous values was the value that maximizes the sum of the sensitivity (true positive rate) and specificity (true negative rate) (Liu et al. 2005). For the global climate model and the hierarchical (global + US) model, predictions were validated using the presence/absence surveys from within the LTB. For the local disturbance/dispersal model, a 10 fold cross-validation procedure was used so that an independent assessment of accuracy could be calculated. The data were split into 10 equal sized groups maintaining the prevalence of the entire dataset within each group. Models were iteratively built with 9 of the groups and the predictive accuracy of the model was evaluated with the held-out group. The final reported accuracy is the mean accuracy across the held-out groups.

Sensitivity to future climate change

Two measures can be used to detect the sensitivity of predictions to climate change. First, the mean climatic suitability of the entire surface for each contemporary and future prediction across the entire Lake Tahoe basin shows whether the suitability is increasing on average. Using the binary predictions from the SDM we can also calculate how the area predicted as present changes through time. To quantify if the local and global contemporary climate data are within or outside the range of the simulated future climate data, we calculated the standardized Euclidean distance between each dataset (local or global) and the future climate:

$$SED_{ij} = \sqrt{\sum_{k=1}^{3} \frac{(b_{ki} - a_{kj})^2}{s_{kj}^2}}$$

where a_{ki} and b_{kj} are the values of the simulated future climate and the contemporary climate variable k, respectively, at grid points i and j and s_{kj} is the standard deviation of the variability of climate variable k

across occurrences in the contemporary data . We allow a liberal comparison for the Tahoe data in that we compare each grid cell in the future simulated climate to every grid cell within the LTB's contemporary climate to show how well a perfect survey of the entire basin would sample for future climate. In contrast, for the global data set, we compare each grid cell from the future simulated climate (in the LTB) to the climate sampled at all occurrence and background points (contemporary conditions). In both cases, the analysis finds the location in the current data set (local or global) with the minimum SED for each simulated future grid cell. Low values of SED indicate that the simulated future climate is included within the sampled range of the contemporary climate while high values of SED indicate future grid cells where a model will be forced to extrapolate beyond the contemporary data.

Results

Contemporary distribution model accuracy

SDM predictions from models calibrated using data from the LTB (local model) had the highest accuracy. The local climate model had an AUC of 0.78, a 14% omission error and a 26% commission error while the global climate model had an AUC of 0.68 a 28% omission error and a 29% commission error (Figs. 2-3). The local disturbance/dispersal model had the highest accuracy with an AUC of 0.80, a 6% omission error and a 23% commission error. The accuracy of the hierarchical model was intermediate with an AUC of 0.70, an omission error of 38% and commission error of 20% (Fig. 4). We have less confidence in the estimated accuracy of the local models as they are based on a partitioned training/test dataset while the test data for the global and hierarchical models are independent from the training data.

Response to predictor variables

The global and local climate models generally agreed in the predicted response of cheatgrass to climate variables. Both models predict a negative response to increasing winter precipitation, with lower than average predicted suitability for winter precipitation greater than 500mm (Fig. 5). Both models also predict increased suitability in response to warming temperatures with optimum winter temperatures near 0°C and optimum summer temperatures around 16° C (Fig. 5). However the predicted response to temperature is truncated under the local climate model as the warmest winter mean temperature in the LTB is -0.66 °C and the warmest summer mean temperature in the LTB is 16.46 °C. Future climate models predict warming from 1.5 °C to 3 °C for the LTB, meaning that the local climate model would need to extrapolate predictions beyond the range of the calibrations under these warmer scenarios.

The relative influence of the predictor variables is reversed between the local and global models. The global model predicts that temperature is more important than precipitation with winter and summer temperature accounting for 73.5% of the relative influence while the local climate model predicts that precipitation is more important with summer and winter precipitation combining to account for 76.9% of the relative influence. Both models find that winter precipitation is more important than summer precipitation with the winter precipitation under the local climate model accounting for 53.59% of the relative influence

Non-climatic factors also have large explanatory power for predicting the distribution of cheatgrass. Both the local disturbance/dispersal model and the hierarchical model find distance to urban areas to be the most important non-climatic variable in predicting the distribution of cheatgrass. Highest predicted suitability occurs within 2 km of urban areas with suitability rapidly decreasing as distance to urban areas increases (Fig. 4), although models also show a smaller increase in suitability at further distances, around 12 km in the hierarchical model and at around 6 km in the local disturbance/dispersal model. The response to roads was similar to the response of urban areas in both models with highest predicted suitability within 1 km of the road with the local disturbance/dispersal showing a steeper decline in suitability as distance increased. For the hierarchical model, predicted suitability is highest between 0 - 20% tree cover then declines to moderate suitability between 20 - 60% tree cover and then steeply declines over 60% cover. The response in the local disturbance/dispersal model is similar except that predicted suitability is greatest at 0 - 40% tree cover but declines steeply when there is greater than 40% tree cover. There is an interaction between the climate niche and distance to urban areas where suitability is substantially higher at low to moderate climate niche suitability when near urban areas. This interaction is most pronounced between climate suitability scores between 0.3 - 0.6, the region that encompasses the threshold (0.581) between predicted present and absent.

Climatic suitability of the Lake Tahoe Basin for cheatgrass, current and future

All models predicted distributions of cheatgrass within the LTB that match closely with the local precipitation gradient, where highly suitable areas correspond to drier and warmer regions (Figs. 2 - 4). The global model predicts higher suitability than the local model within the LTB under both current climate and future climate scenarios (Figs. 2, 3, 7). However, the predictions from presence-only models (global climate model) and presence/absence models (local climate model) are not directly comparable so we must be cautious with over-interpreting the difference. Binary predictions from the two models are comparable though. The local climate model predicted more of the LTB to be presently suitable than the global climate model (local model = 10812 200m^2 cells, global model = 6932 200m^2 cells).

For future climate scenarios, the local climate model generally predicts contracting areas of suitable habitat (Figs. 7 - 8). While there is considerable variation in the change in future suitable area under the global climate model, it tends to predict greater area of suitability than the local climate model. For example, using the CCCma CGCM3.1 GCM, the global climate model predicts expanded suitability for every 5 year time step except 2060 while the local climate model predicts contracting suitability in 6 of the 9 time steps (Fig. 8). The total area predicted as climatically suitable is highly variable under future climate simulations. There is little agreement among the predictions from GCMs tested here suggesting that the distribution of cheatgrass is sensitive to climate variables that have uncertain future projections (Figs. 7 - 8).

Novel climate

There are areas within the LTB in which future climate is projected to have no contemporary climatic analog within the LTB. High SED values indicate areas where models are forced to extrapolate predictions beyond the range of the training data to predict future suitability. The results show that the *local models* of climate are forced to extrapolate predictions to climate simulations over much of the basin. By looking at the map of the minimum SED we can pinpoint locations where prediction errors may be most egregious (Fig 9). Some of the highest climatic dissimilarity (large minimum SED) values occur on the west side of the Lake Tahoe basin and correspond with areas not predicted to be highly suitable by the local climate model in either the current or future predictions (Fig. 9). However, the minimum SED for the *global mode*l is low across the entire basin (Fig. 9) meaning the global models do not have to extrapolate when predicting to future climate conditions.

Discussion

In support of our first hypothesis, drier sites, especially those highly disturbed (e.g., close to roads and urban areas), were more suitable for cheatgrass than wetter, undisturbed sites. The majority of the cheatgrass occurrences located in our survey of 241 sites were along the south and east shores (Fig. 1), where precipitation is relatively low and summer temperatures are mild. With some local exceptions, cheatgrass did not generally occur along the west and north shores. More locally, we noted during our field survey that cheatgrass was often found on the edge of meadows, but not in the middle where soil moisture levels were higher. Accordingly, the distribution of highly suitable areas for cheatgrass in the LTB based on the local model closely follows the west to east decline in precipitation (Fig. 2). Interestingly, the local dispersal/disturbance model predicted cheatgrass occurrence with slightly higher accuracy than climate variables alone. In other words, urban areas and roads are better predictors of the occurrence of cheatgrass than climate on its own. Further, areas with low to moderate climate suitability can have higher overall predicted suitability when they are close to urban areas or roads, highlighting the interaction of climate and disturbance in determining the suitability of sites to cheatgrass invasion. This finding matches observations made in the field that cheatgrass reached maximum prevalence and abundance in sites that were near roads or highly disturbed areas, and its local abundance quickly declined moving away from the disturbance source, consistent with its classification as a ruderal species that follows disturbance. In the global model, temperature was a more important predictor of cheatgrass occurrence than precipitation, but both variables had significant explanatory power. Both global and local models indicate that warmer winter temperatures are better for cheatgrass. Interestingly, the west side has higher annual temperatures, yet this area is of low predicted suitability for cheatgrass due to the higher levels of precipitation. In biological terms, this may imply that cheatgrass can physiologically tolerate the higher temperatures, but the combination of warm temperatures and high precipitation in these areas leads to higher productivity, which may result in the exclusion of cheatgrass by competitors. These results combine to suggest that cheatgrass in the LTB is controlled primarily by precipitation and proximity to dispersal corridors and disturbances, but temperature, especially average minimum winter temperatures, are also important for determining when cheatgrass establishment can initially occur.

In support of our second hypothesis, there are large areas within the LTB that are climatically suitable for cheatgrass, but do not yet contain the species (Fig. 3). Our global species distribution model of cheatgrass, which more closely reflects the physiological tolerances (or fundamental niche) of the species, showed that climatic niche conditions suitable for cheatgrass establishment are widespread in the LTB, but especially on the east side (Fig. 3). On the contrary, the west and north sides of the basin had low suitability for cheatgrass establishment, meaning that precipitation and temperature conditions may be outside of the physiological tolerances of the species or that the competitive advantages under cooler and drier conditions no longer apply due to the higher productivity of competitors in warmer and wetter areas.

Perhaps the most useful model outputs for early detection of cheatgrass establishment come from the hierarchical (global + US) model, which incorporates both climate and non-climate factors into predictions of cheatgrass suitability (Fig. 4). Maps of the continuous predictions of the hierarchical model show more widespread moderate to high suitability predictions than the other models (Fig. 4). This suggests that a considerable amount of area is currently suitable, but unoccupied by cheatgrass, within the LTB. Consistent with the individual local and global models, the hierarchical model shows high suitability in drier sites, but also identifies areas that are marginally suitable climatically but are near enough to dispersal corridors or disturbed sites to be categorized as being at high risk of cheatgrass establishment (Fig. 4). In other words, areas with moderate climate suitability can have higher overall predicted suitability when close to urban areas or roads. These sites may be especially prone to invasion if climate changes to favor cheatgrass establishment. To avoid substantial spread into these unoccupied but suitable areas, care should be taken to limit anthropogenic dispersal of cheatgrass seed as well as to minimize disturbances that will remove native plant cover or disturb soils, thereby facilitating the establishment of cheatgrass.

The binary predictions of the hierarchical model, however, show less area as being suitable for cheatgrass, but also have the highest degree of underprediction (false negatives). Thresholds for converting continuous predictions to binary presence and absence are determined based on tradeoffs between false positive and false negative predictions. Even accurate models will have a high degree of false positive predictions (overprediction) if cheatgrass is dispersal limited (i.e., propagules have not yet arrived at all climatically suitable sites) and/or non-climatic factors prevent its establishment (e.g., climatically suitable sites within the seed rain of cheatgrass are unoccupied because of strong biotic resistance or a lack of disturbance). Thus presence/absence thresholds may be higher to balance the apparent overprediction under dispersal limitation. The high omission error (underprediction) of the hierarchical (global + US) model is caused by the high threshold value (0.899) selected to minimize overprediction.

Our climate forecasts suggest climatic suitability for cheatgrass will continue to be high for the LTB into the next 20 years (Fig. 5) and up to 60 years (see GIS). Most notably, low precipitation areas (south and east shores) are consistently suitable across time and models. This suggest that invasion will proceed most quickly and uninterrupted in these areas, providing source populations for new invasion elsewhere in the LTB in the foreseeable future. However, in general, the high levels of precipitation in many of the currently unsuitable sites are forecasted to remain sufficiently high in the future to prevent many of these areas from becoming climatically suitable for cheatgrass. Also, winter temperatures are not predicted to increase drastically in the LTB in the near term, so a large increase in climatic suitability is not expected. Interestingly, other areas within the LTB are highly variable in suitability through time. These sites are currently near the edge of being climatically suitable, and interacting effects of changing precipitation and temperature in the future causes suitability to cyclically move above and below the level of suitability theoretically required for invasion (Fig. 6). Contractions of areas of projected suitability should not be interpreted as indicators of future cheatgrass disappearance! It is very possible that cheatgrass can persist in the seed bank and in local microsites through periods of climate unsuitability. Further, climate predictions are not modeled with high accuracy or precision by global climate models for mountain environments, especially for precipitation (IPCC, 2007), and thus our results only roughly estimate the potential expansion of suitable climates and should be revised upon the release of improved regional climate models. While our modeling suggests that overall climatic suitability for cheatgrass may not increase dramatically over the next 60 years, landuse and management choices will influence disturbance and dispersal factors that directly affect cheatgrass invasion.

There are areas within the LTB in which future climate is projected to have no contemporary climatic analog within the LTB, according to the local model (Fig. 7). For these sites, the accuracy of predictions made by the local model may be highly uncertain. However, many of the sites projected to support no-analogue climates are not predicted to be highly suitable for cheatgrass, because the forecasted no-analog climates do not contain optimal conditions that aren’t already present in the LTB. The global model does not need to extrapolate when making future predictions, and hence is likely a more accurate tool to use in examining changes in climatic suitability for cheatgrass over time in the LTB, especially over long time scales.

Conclusions

The most effective way to reduce the impact of invasive species is to identify new occurrences and eradicate them. In the beginning of an invasion, there is a window of opportunity where eradication is possible and economically feasible. Recent observations by botanists suggest that cheatgrass distribution and abundance are increasing strongly in the LTB. This puts a premium on early detection programs, designed to identify areas at high risk of invader establishment. Cheatgrass is one of the most notorious invasive species in North America, causing dramatic and apparently irreversible degradation of natural communities. In the LTB, there may yet be a chance to control cheatgrass invasion before it gets out of hand. Our spatially explicit model of invasion risk for the LTB, available as a GIS, is a tool that allows managers to predict where invasion is currently most likely. For any given spot in the LTB, the cheatgrass suitability score is available and can be used as a continuous or binary description of the risk of a given site for cheatgrass invasion, based on climatic suitability alone or climate and disturbance factors combined. This product identifies the high-risk areas where early detection campaigns may be most successful. As climate changes, these models can be applied to climate layers of the new conditions in the LTB to refresh the predicted site suitability. While a great deal of uncertainty remains in forecasting the magnitude and even direction of climate change for LTB, our current GCM-based models suggest that if drying or warming occurs, an increase in the suitability of the LTB for cheatgrass will follow. Note that expansive areas of suitable, unoccupied areas do exist today. Some of these areas are within planned forest thinning or meadow restoration treatments, and some of these areas may also be burned in unplanned wildfires in the future. We believe that it is imperative to carry out preproject inventory of invasion in these sites and to monitor the effects of these projects on cheatgrass invasion after treatment. Burned areas should also be monitored for cheatgrass presence. Quick action should be taken if cheatgrass establishment is documented. Particular attention should be paid to areas identified as high-risk in our GIS models of current invasion risk. As temperatures warm and cheatgrass suitability rises (if and where it does), the threat of enhanced fire activity will rise with it. Much appears to depend on future patterns of precipitation in the LTB, but whatever happens, we believe it is in the best interest of resource managers to monitor for cheatgrass, rather than simply to treat it as inevitable. Some level of cheatgrass presence may indeed be inevitable in the LTB, but ignoring the threat of further invasion and the factors that abet it could lead to serious ecosystem consequences.

Acknowledgements

We acknowledge the modeling groups, the Program for Climate Model Diagnosis and Intercomparison (PCMDI), and the WCRP's Working Group on Coupled Modelling (WGCM) for their roles in making available the WCRP CMIP3 multi-model dataset.

This research was supported by a cooperative agreement with the USDA Forest Service Pacific Southwest Research Station, using funds provided by the Bureau of Land Management through the sale of public lands as authorized by the Southern Nevada Public Land Management Act. The views in this

report are those of the authors and do not necessary reflect those of the USDA Forest Service Pacific Southwest Research Station or the USDI Bureau of Land Management.

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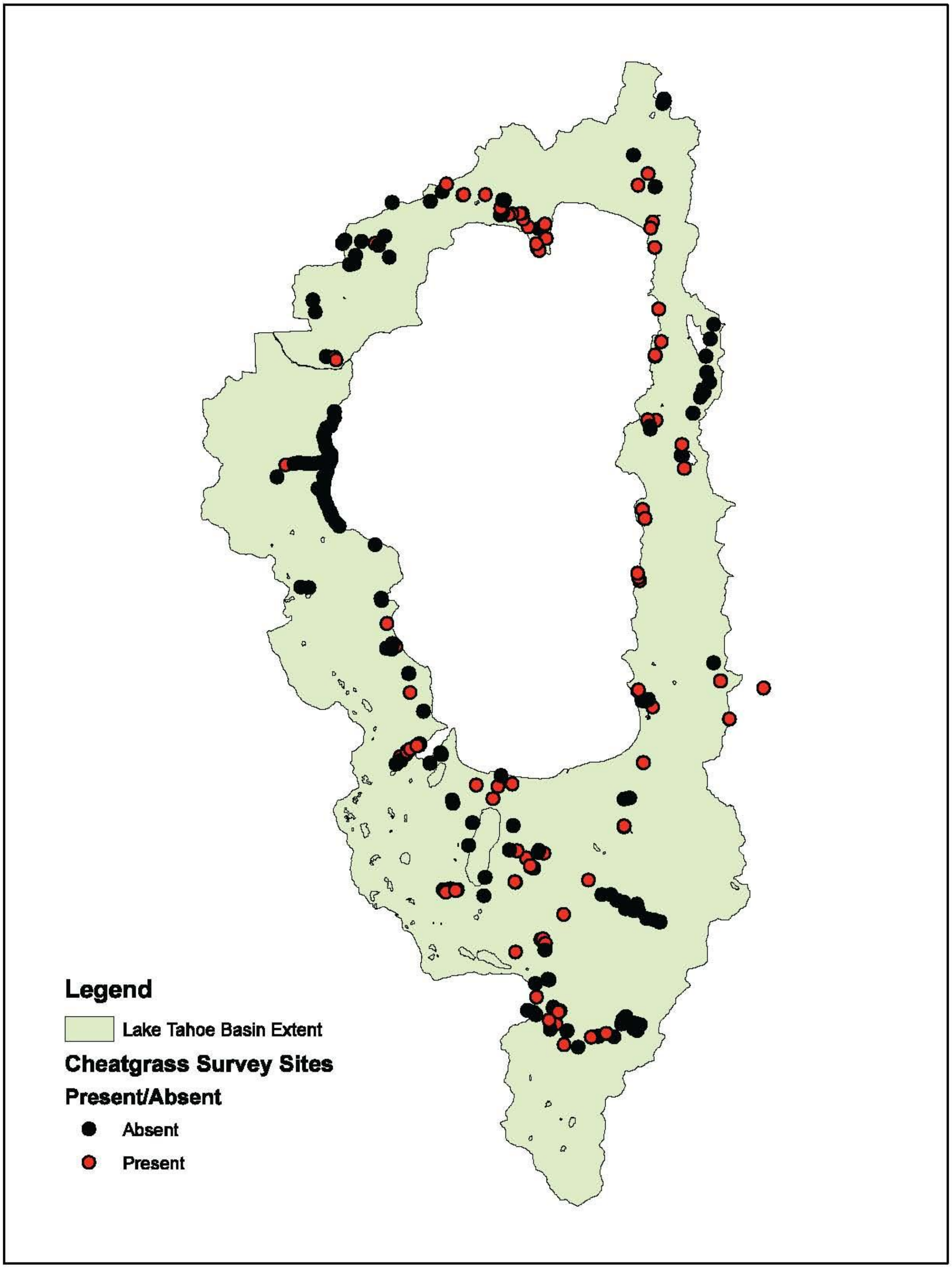

Fig. 1. Map of 241 sites visited to assess cheatgrass occurrence.

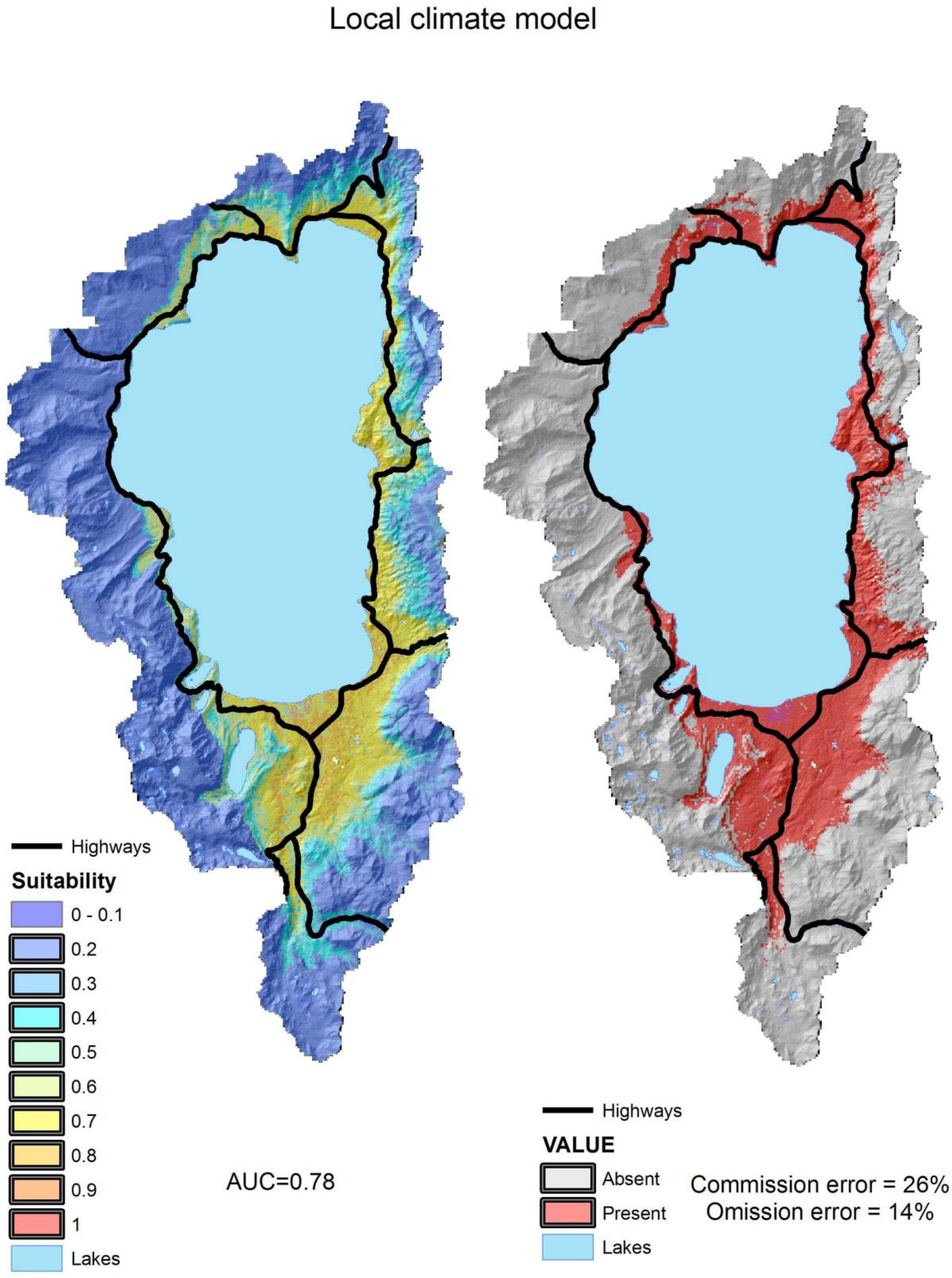

Fig. 2. Map of current climatic suitability for cheatgrass, based on a species distribution model trained on the field collected cheatgrass occurrence data (the "local" model). For Figs. 2 – 4, the left panel is a map of suitability as a continuous variable and the right panel is a map of suitability as a binary variable, where the threshold value chosen is the value that maximizes the sum of the sensitivity (true positive rate) and specificity (true negative rate).

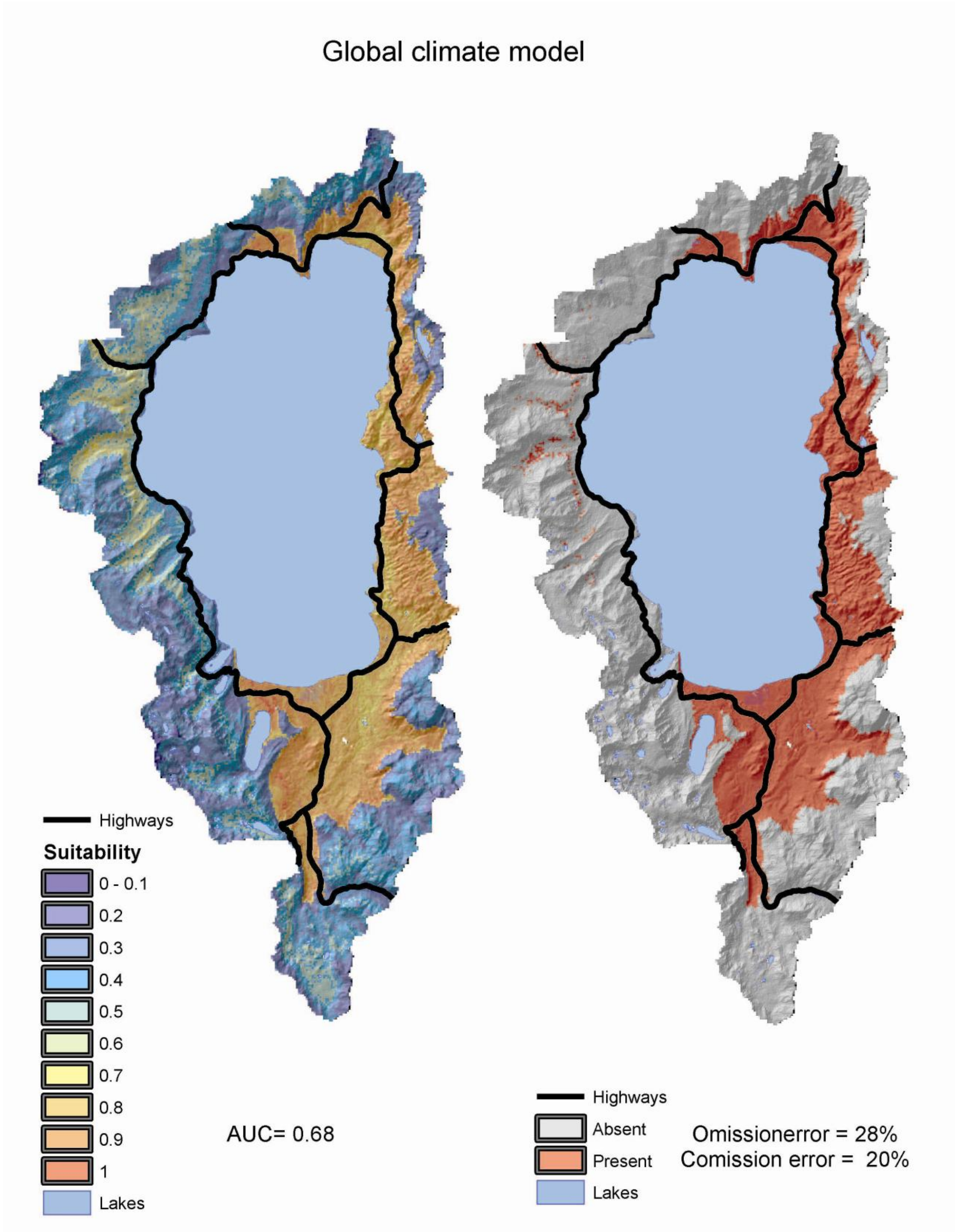

Fig. 3. Map of current climatic suitability for cheatgrass, based on the species distribution model trained on the global cheatgrass occurrence data (the "global" model).

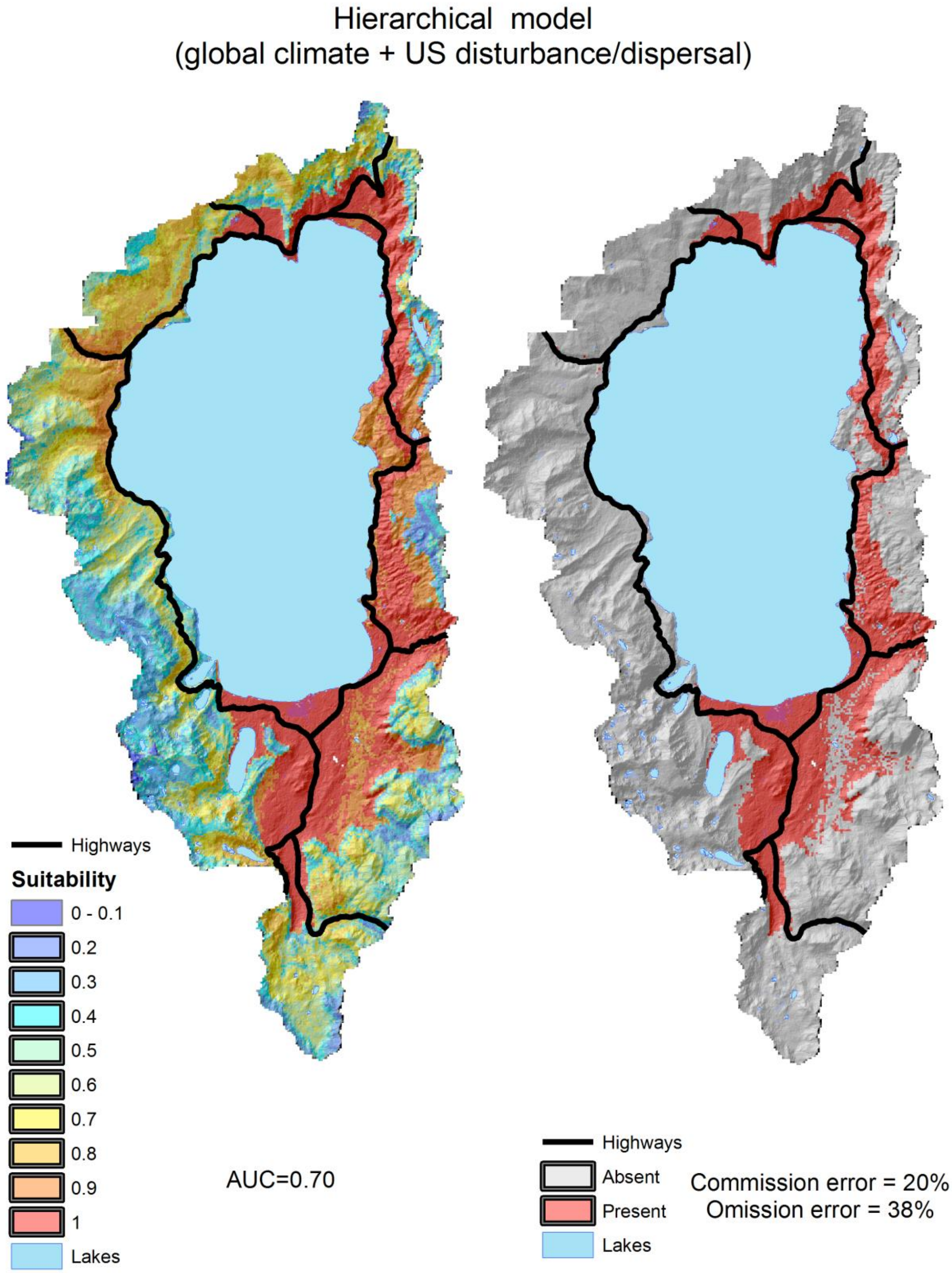

Fig. 4. Map of current suitability for cheatgrass based on a species distribution model trained on global climate variables and US disturbance/dispersal variables (the "hierarchical (global + US)" model).

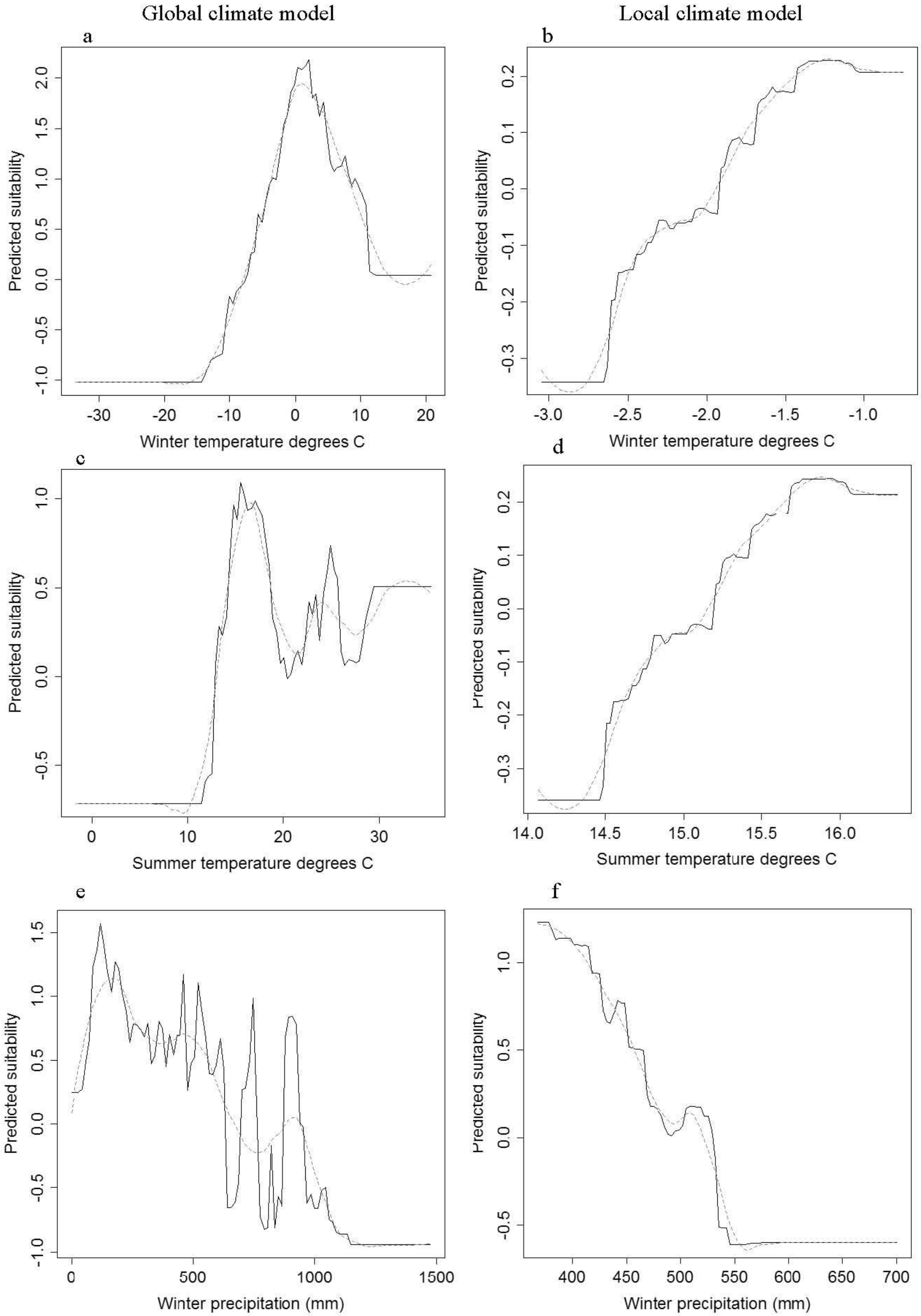

Fig. 5. Plot of the predicted response to climate variables while holding each of the other variables constant. For Figs. 5 – 6, predicted values are scaled to have a mean of zero. The red dashed line is a smoothed fit to the curve.

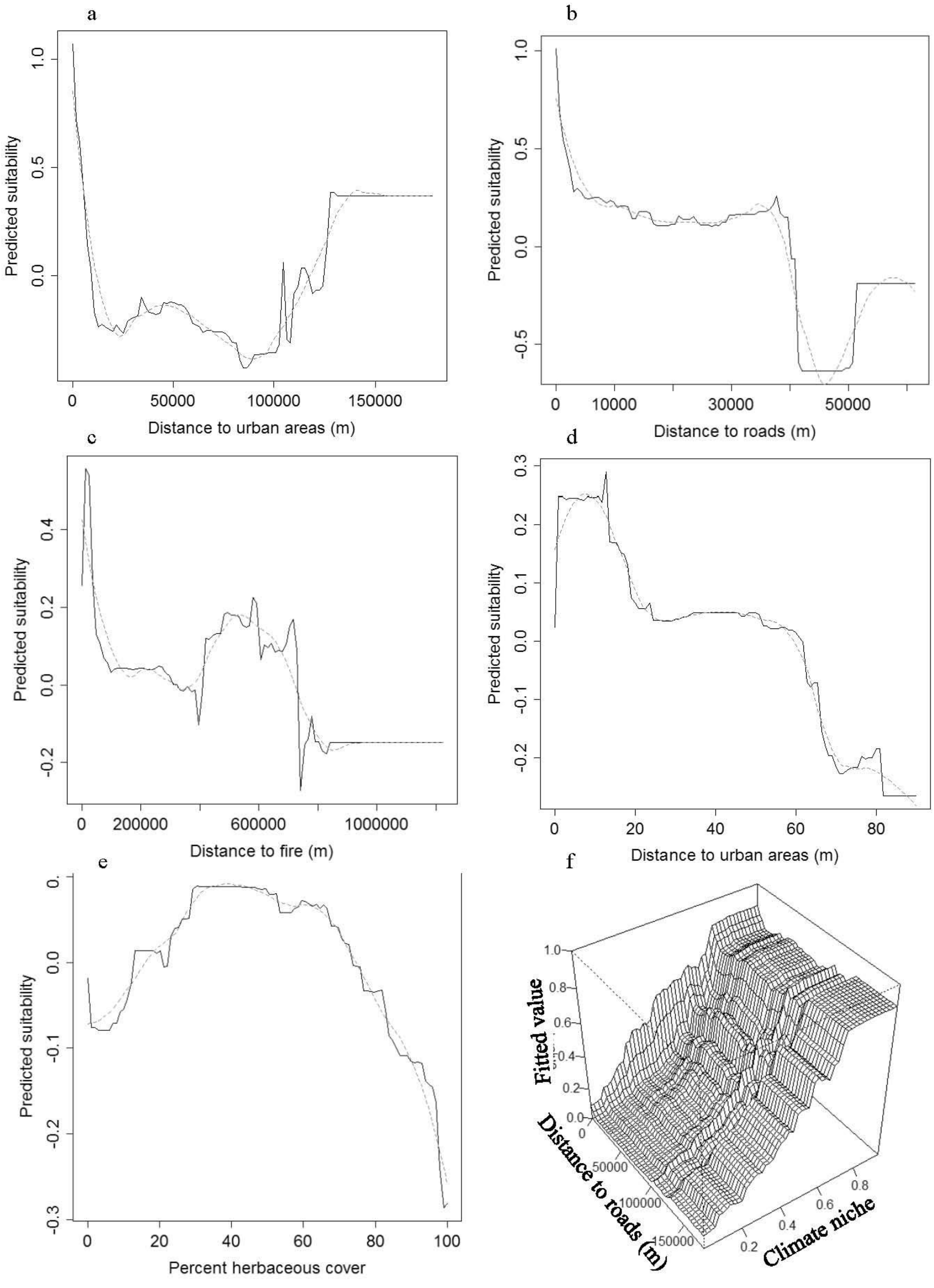

Fig. 6. Plot of the predicted response to the non-climatic variables (a-e) and the interaction between the climate niche and the distance to urban areas (f). Higher fitted values equal higher suitability.

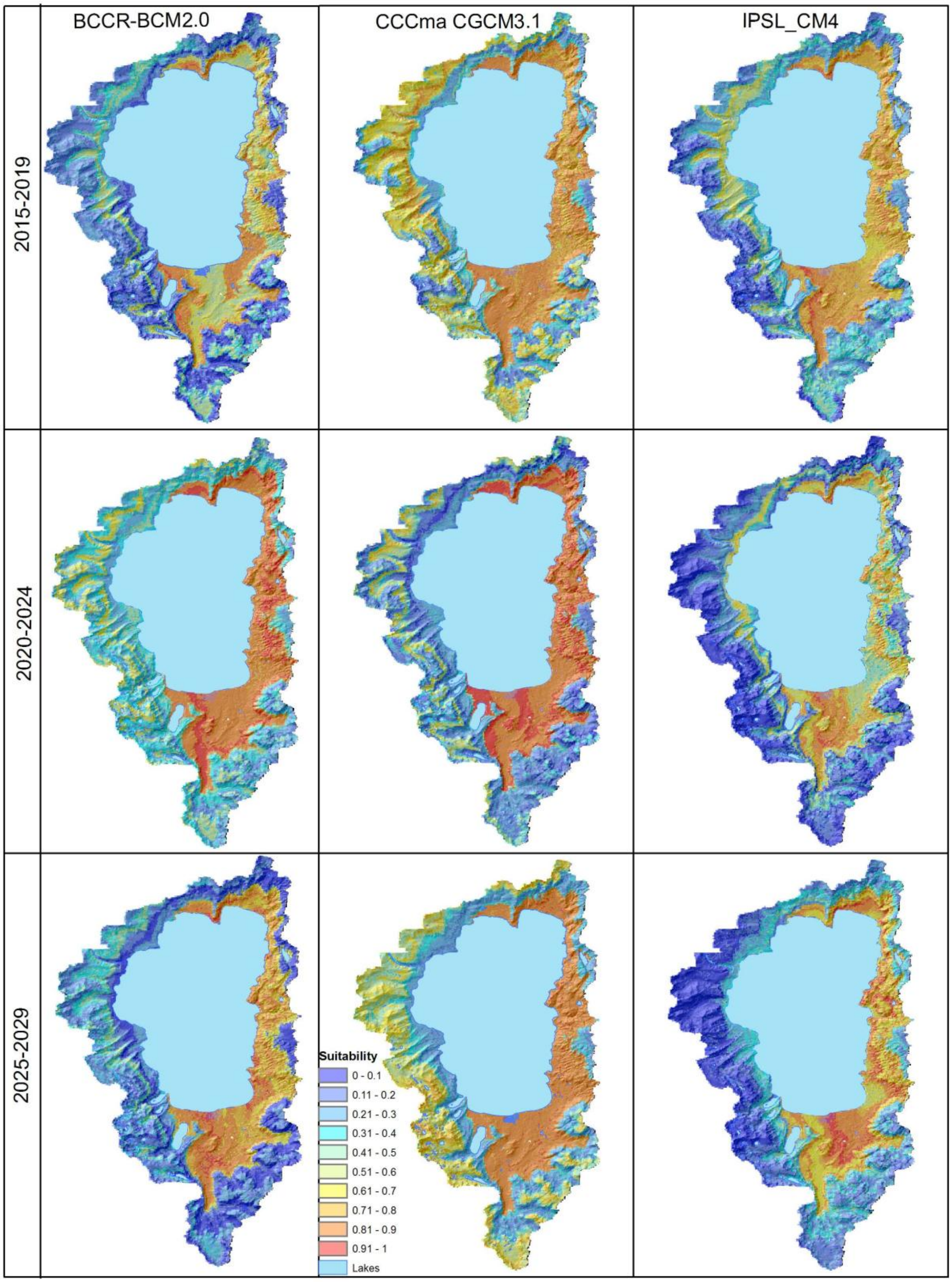

Fig. 7. Maps of predicted suitability at three time intervals (rows) for each of three circulation models (columns).

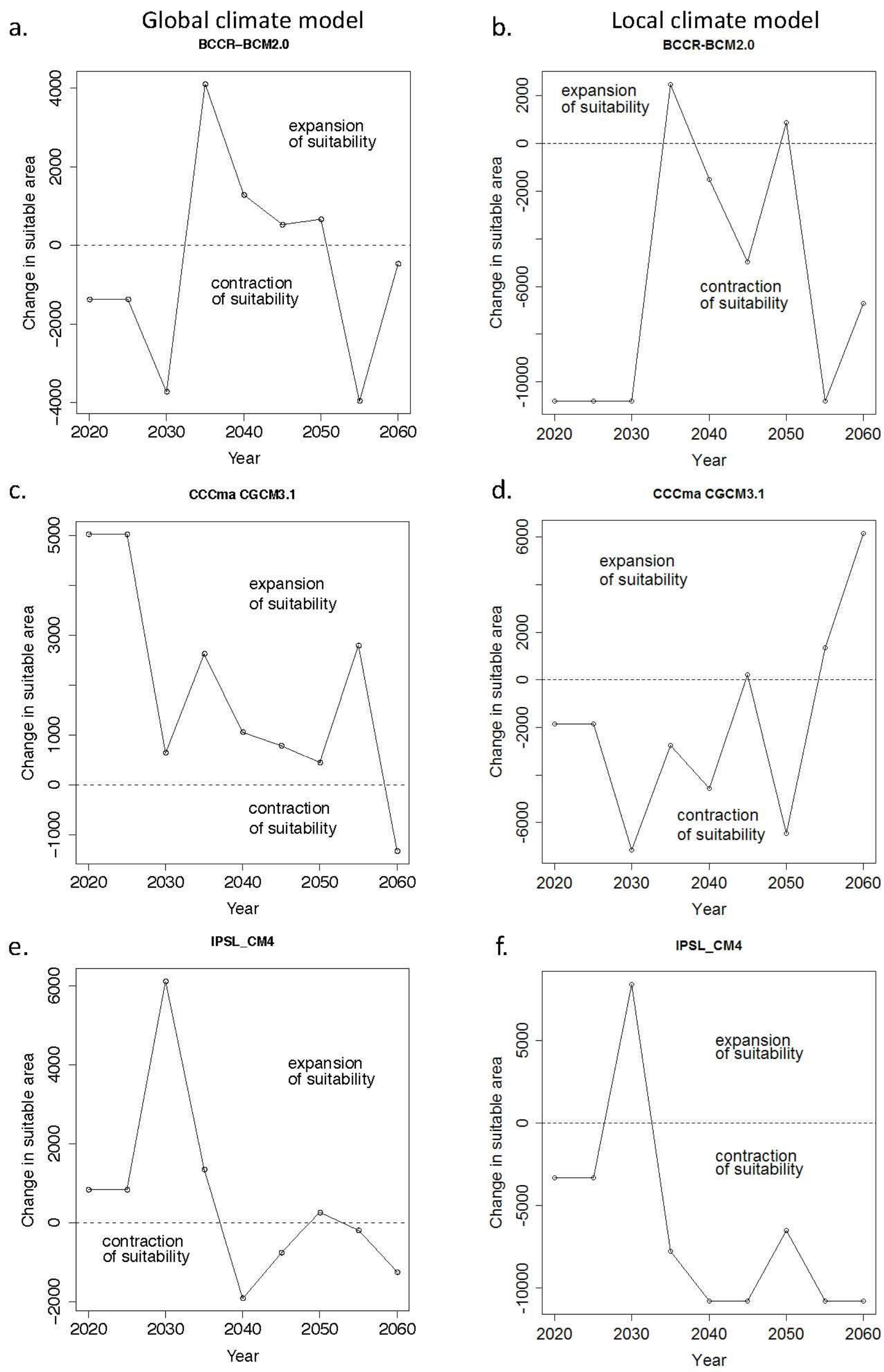

Fig. 8. Plots of the change in total suitable area for cheatgrass over time for each of three circulation models and two species distribution models. Points above the dashed line indicate that the total area predicted as suitable for cheatgrass increased from the previous time point; vice versa for points below the dashed line.

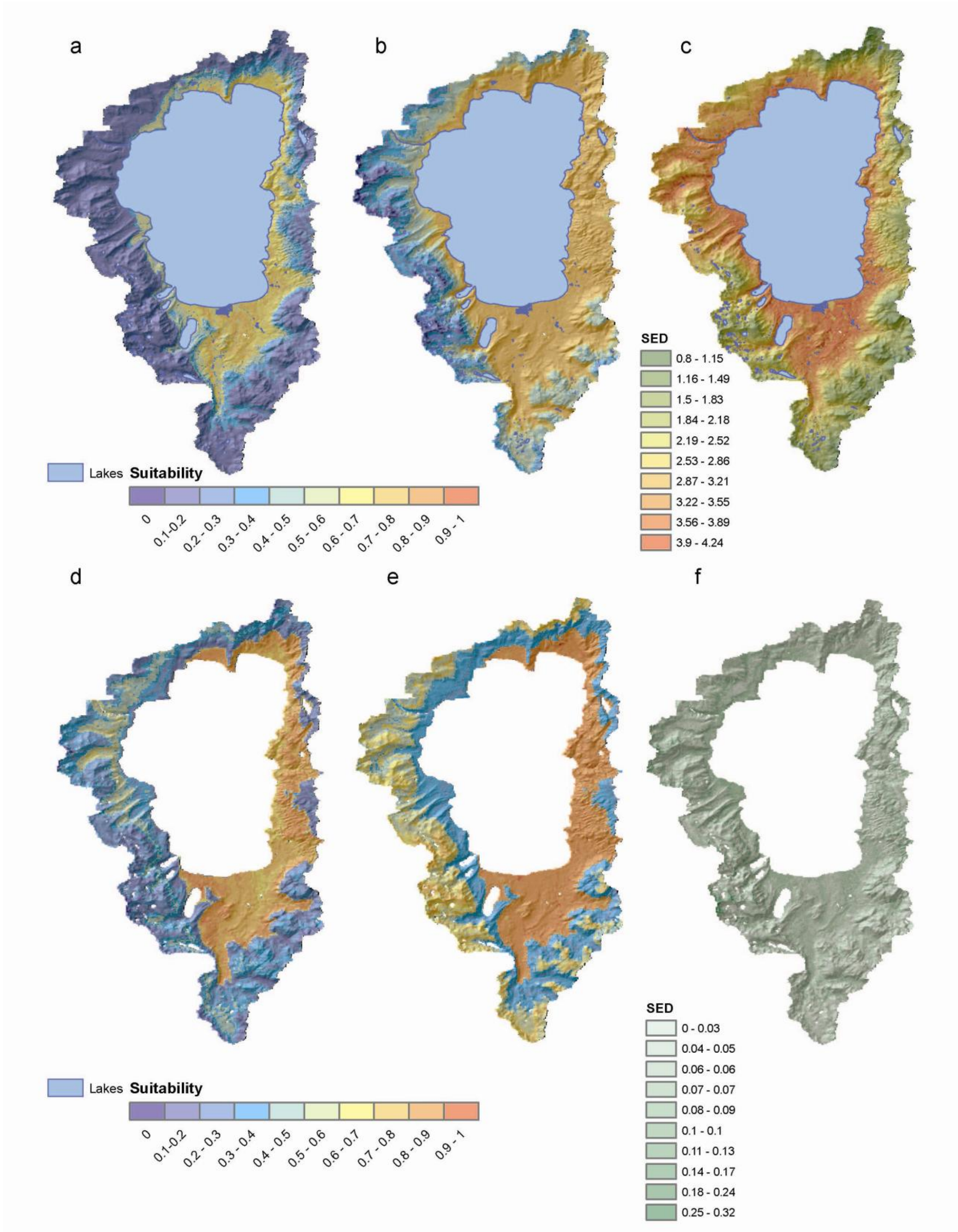

Fig. 9. Climatic suitability and novel climates. Upper row: Current climatic suitability (a), future climatic suitability (b), and similarity between current and future climate (c) from the *local model*. Lower row: Current climatic suitability (d), future climatic suitability (e), and similarity between current and future climate (f) from the *global model*. High SED values indicate areas where models are forced to extrapolate predictions beyond the range of the training data to predict future suitability.