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RESEARCH ARTICLE

Regional climate model downscaling may improve the prediction of alien plant species distributions

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Abstract Distributions of invasive species are commonly predicted with species distribution models that build upon the statistical relationships between observed species presence data and climate data. We used field observations, climate station data, and Maximum Entropy species distribution models for 13 invasive plant species in the United States, and then compared the models with inputs from a General Circulation Model (hereafter GCM-based models) and a downscaled Regional Climate Model (hereafter, RCM-based models). We also compared species distributions based on either GCM-based or RCM-based models for the present (1990–1999) to the future (2046–2055).

RCM-based species distribution models replicated observed distributions remarkably better than GCM-based models for all invasive species under the current climate. This was shown for the presence locations of the species, and by using four common statistical metrics to compare modeled distributions. For two widespread invasive taxa (*Bromus tectorum* or cheatgrass, and *Tamarix* spp. or tamarisk), GCM-based models failed miserably to reproduce observed species distributions. In contrast, RCM-based species distribution models closely matched observations. Future species distributions may be significantly affected by using GCM-based inputs. Because invasive plants species often show high resilience and low rates of local extinction, RCM-based species distribution models may perform better than GCM-based species distribution models for planning containment programs for invasive species.

Keywords climate change, species distribution model, Maxent, downscaling

1 Introduction

Climate determines regional- to global-scale plant distributions, and recent climate change has already significantly affected plant species distributions (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003). Projected climate changes of a significant magnitude (IPCC, 2007) may have even greater impacts on plant distributions (Thomas et al., 2004; Yates et al., 2010).

Invasive plant species are regarded as one of the most serious global-scale environmental threats of the 21st Century (Beaumont et al., 2009). They can have significant negative impact on native biodiversity (Bellard et al., 2012), cause significant economic losses to crop and timber production (Mack et al., 2000; Pimentel et al., 2005), and they disrupt ecosystem services (Cook et al., 2007). As the atmospheric CO_2 concentration increases and the prevailing climatic zone shifts, alien plant species may out-compete native species and spread into previously unoccupied habitats (Beaumont et al., 2009; but see Holcombe et al., 2010). Given that the eradication of an established invasive species is extremely expensive (Pimentel et al., 2005), it is useful to be able to predict their potential distributions before they become large problems (Rejmánek and Pitcairn, 2002; Stohlgren and Schnase, 2006).

Species distribution models have been widely used to simulate and predict the potential distributions of harmful invasive species (Thuiller et al., 2005; Elith et al., 2006; Kumar et al., 2009). Statistical correlative species distribution models describe suitable habitats for a species in terms of probabilities (Phillips et al., 2006; Elith and

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Leathwick, 2009; Elith et al., 2011). Assuming that species-environment relationships do not change over time, and excluding other biotic interactions, a species' future distribution may be modeled using climate change scenarios (e.g., Thuiller, 2003; Thomas et al., 2004; Holcombe et al., 2010).

There are many caveats to species distribution models. The accuracy of such models is dependent on data sample sizes (Stockwell and Peterson, 2002), species range sizes (McPherson et al., 2004; Segurado and Araújo, 2004), and modeling techniques (Pearson et al., 2006). The impact of climate data quality may also be an important consideration in species distribution modeling In order to project a reasonable future distribution, the indispensable bioclimatic variables for species distribution model input must be reliable.

Many investigators rely on future bioclimatic variables that are either statistically derived from current sparse station observations (e.g., Thornton et al., 1997; Hijmans et al., 2005) or are simulated by coarse-scale (0.5 to > 4 degree grids) General Circulation Models (GCM; e.g., Hijmans et al., 2005). Coarse-scale bioclimatic information may be insufficient or inconsistent for species distribution models derived from finer-scale species occurrence data. The dynamic Regional Climate Model (RCM) is a powerful tool that incorporates a more comprehensive representation of regional physical processes and finer model resolutions that translate coarse-scale simulations into the more reliable predictions of surface climate variables that are essential to modeling species distributions. The RCM's results have been widely shown to outperform coarse-scale simulations by more realistically reproducing observed climate, and thus, they produce more credible future projections (Liang et al., 2004, 2006, 2012). The regional model approach, extensively used in the climate change community, rarely has been used in species distribution modeling (Franklin et al., 2013).

We quantify how the quality (or coarseness) of the input climate data can affect predictions of species distributions by comparing the results based on either the General Circulation Model (GCM-based) or regionally downscaled climate (RCM-based) data. We evaluate the accuracy of the fitted species distribution models compared to the current and projected future distributions of 13 invasive plant species.

2 Data and method

A generalized flowchart shows how we build a species distribution model on a given bioclimatic dataset (Fig. 1). The raw species presence data are randomly split into training (80%) and test (20%) data. For a given climate dataset, a species distribution model is first built based on the training data for the species in question, and makes a projection on the test data to assess the model's accuracy. The same model is re-run with either GCM-based data or RCM-based data for the current time or future scenarios to predict changes in suitable habitat for a given invasive plant species.

2.1 Climate and species data

We used three climate dataset types. The GCM-based data are from the simulations conducted by the National Center for Atmospheric Research Community Climate System Model Version 3 (CCSM3, T85, ~1.4°C; Collins et al., 2006). The RCM data are drawn from dynamic downscaling from the same GCM simulations conducted by the Climate extension of the fifth-generation Pennsylvania State University-NCAR Mesoscale Model (CMM5, 30 km; Liang et al., 2004). The "observed" daily precipitation and temperature data (for our reference models) are based on an objective analysis of measurements from 7,235 National Weather Service stations across the U.S. (Liang et al., 2004). Six bioclimatic variables (Nix, 1986) were derived from surface air temperature and precipitation: annual mean temperature, mean temperature diurnal range, minimum temperature of coldest month, annual precipitation, precipitation seasonality, and precipitation of driest quarter. These variables represent general trend (means), variation (seasonality), and limiting factors (minimum and maximum temperatures).

We selected two 10-year periods, 1990–1999 and 2046–2055, to represent present and future climate conditions. The future projections were based on the Intergovern-

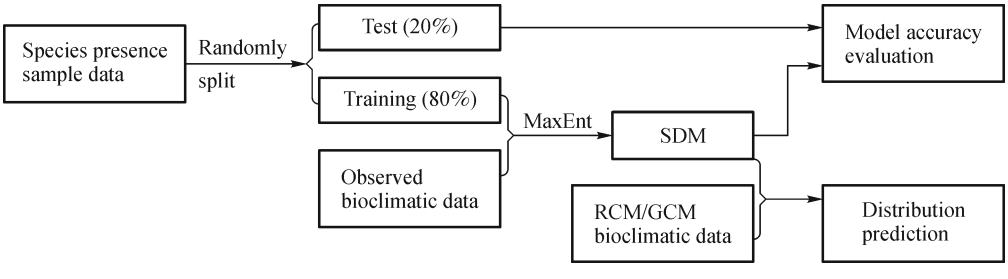

Fig. 1 Flowchart illustrating key steps of building, testing, and applying a species distribution model for predicting the geographical distribution of a typical invasive plant species.

mental Panel on Climate Change (IPCC, 2007) A1FI (fossil fuel intensive) emission scenario, in which the CO_2 concentration was projected to reach approximately 567 ppm at 2050. For consistency, temperature and precipitation data from observations and GCM simulations were first mapped to the RCM's 30 km×30 km grid using bilinear interpolation. The bioclimatic variables were then calculated on this grid for coarse-scale GCM-based and downscaled RCM-based species distribution models. These models were run for each species relative to the observed bioclimatic variables. The performance of the GCM-based and RCM-based species distribution models were tested by comparing the differences in suitable habitat compared to results driven by the observed climate variables.

The presence data for 13 alien invasive species (not native to the U.S.; Table 1) were obtained from the National Institute of Invasive Species Science (NIISS, www.niiss.org). The species were selected because they are present in different climate regimes across the U.S., and also because they have various sample sizes distributed over narrow or broad areas. To reduce the potential bias of clustered occurrences, the presence points were first spatially filtered in order to remove duplicates so that only one record within each 30 km×30 km grid cell remained. This process resulted in total sample points ranging from 27 (Yellow toadflax) to 987 (Tamarisk) (Table 1), and samples were distributed across the study domain, which contained 8,471 grid cells (Fig. 2).

2.2 Maxent species distribution model

Among many of the species distribution model fitting techniques, Maxent (version 3.3.3k; http://www.cs.princeton.edu/~schapire/maxent/) is a well tested, well accepted, and commonly used method (Phillips et al., 2006; Kumar et al., 2009; Elith et al., 2011). It has been shown to be a top performing algorithm compared to other methods (Elith et al., 2006; Hernandez et al., 2006, Kumar et al., 2009). Maxent is a machine learning method and uses presence-only data. It estimates the suitability of a habitat for a species by applying the maximum entropy principle and species-environmental relationships (Phillips et al., 2006).

In order to build a species distribution model for a given species, Maxent starts with a uniform probability distribution, and performs a number of iterations, each of which decreases the regularized log loss (objective function). The objective function value decreases iteration by iteration, until the change from one iteration to the next falls below the convergence threshold (1.0×10^{-5} in this study). For more information on the Maxent model, see Phillips et al. (2006). The same model for each of the species is used throughout this paper, only the bioclimatic variables are different for each simulation.

2.3 Evaluation measures

The species distribution models were evaluated in several ways. First, for each model, 20% of the sample data were withheld in model training in order to assess the accuracy of the resultant model. This metric of accuracy is the receiver operating characteristic curve (AUC) based on the derivation of the Wilcoxon statistic (Fielding and Bell, 1997). This curve is obtained by plotting *sensitivity* (the proportion of correctly predicted presences) on the *y*-axis and 1-*specifity* (the proportion of correctly predicted absences) on the *x*-axis for all possible presence/absence thresholds. Thus, AUC provides a threshold-independent metric of model performance. For the presence-only data, as in this study, AUC is the probability that a randomly

Table 1 The 13 invasive species used as study cases (species are listed increasingly according to total sample points)

Common name	Scientific name	Number of sample points			Test AUC
		Total	Training	Testing	
Yellow toadflax	*Linaria vulgaris*	27	22	5	0.98
Buffelgrass	*Pennisetum ciliare*	71	57	14	0.92
Brazilian pepper-tree	*Schinus terebinthifolius*	86	69	17	0.98
Bull thistle	*Cirsium vulgare*	103	83	20	0.91
Dalmatian toadflax	*Linaria dalmatica*	113	91	22	0.92
Russian olive	*Elaeagnus angustifolia*	156	125	31	0.89
Musk thistle	*Carduus nutans*	158	127	31	0.88
Bindweed	*Convolvulus arvensis*	196	157	39	0.91
Russian thistle	*Salsola kali*	205	164	41	0.93
Canada thistle	*Cirsium arvense*	262	210	52	0.88
Cheatgrass	*Bromus tectorum*	534	428	106	0.92
Japanese honeysuckle	*Lonicera japonica*	562	450	112	0.93
Tamarisk	*Tamarix* spp.	987	790	197	0.83

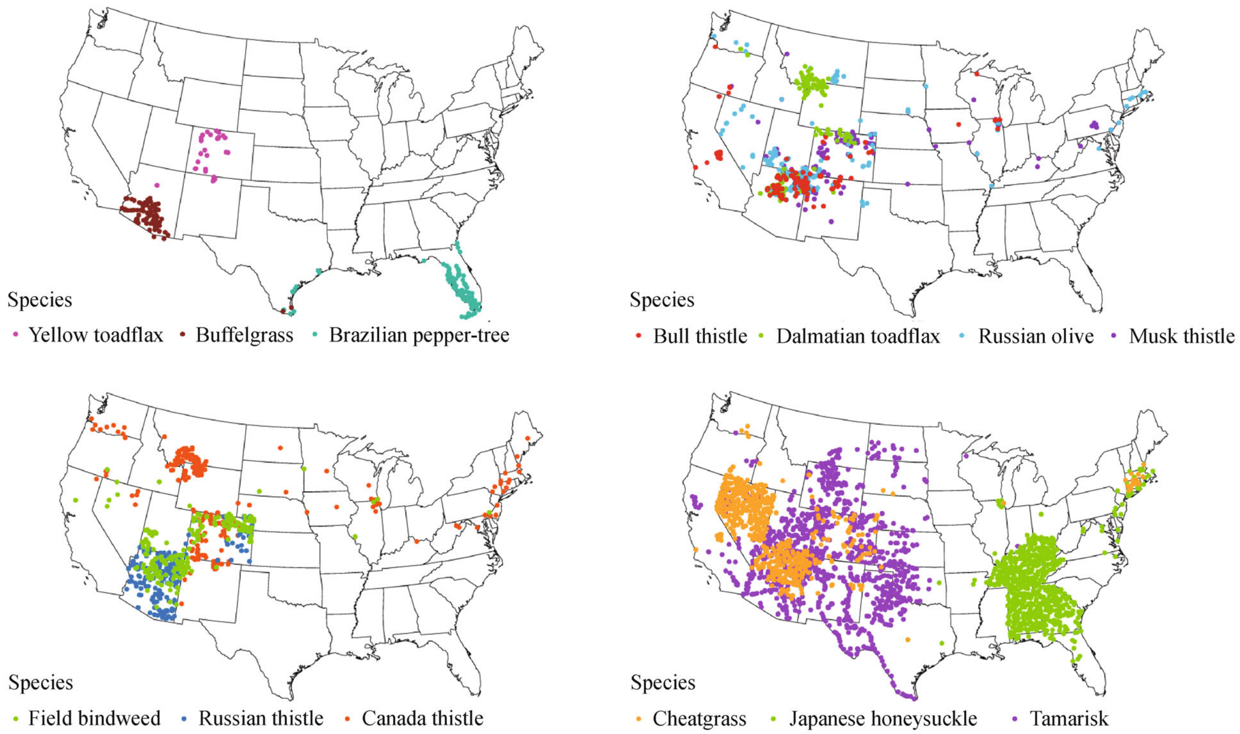

Fig. 2 Geographic distribution of species sample points.

chosen presence site is ranked above a random background site (Phillips et al., 2006). A ranking that is no better than random yields AUC = 0.5, a perfect ranking is AUC = 1.0, while the maximum possible test AUC is typically less than 1 (Wiley et al., 2003; Phillips et al., 2006). The AUC is a generally accepted as a reliable metric when used to evaluate species distribution model performance (Elith et al., 2006) because of its independence of presence threshold. We adopted the interpretation guidelines for model predictive ability as recommended by Swets (1988): AUC > 0.9 for excellent, 0.8–0.9 for good, 0.7–0.8 for fair, 0.6–0.7 for poor, and we considered < 0.6 as no better than random.

A cut-off threshold was defined for each species, above which model outputs (presence probability, ranging continually from 0 to 1) were considered to represent a suitable habitat for the species. Thresholds were defined by maximizing the agreement between the observed and modeled distributions for the sampled data. Sensitivity (the proportion of positive predictions vs. the number of actual positive sites) and specificity (the proportion of true negative predictions vs. the number of actual negative sites) was calculated at thresholds increasing in increments of 0.01 from 0 to 1, and the threshold at which these two values are closest was adopted. This approach balances the cost arising from an incorrect prediction against the benefit gained from a correct prediction (Manel et al., 2001; Liu et al., 2005).

Having defined suitable habitat for a range of species throughout the study region based on the cut-off threshold, we evaluated how well GCM- and RCM-based predictions corresponded to those based on observed climate variables. We evaluated four indices: relative range size, range overlapping rate, false presence rate, and false absence rate (also called missing rate):

$$\begin{aligned}&\text{Relative range size}\\&=\text{Modeled range size}/\text{Observed range size},\end{aligned}$$

$$\begin{aligned}&\text{Range overlapping rate}\\&=\text{Common range size}/\text{Observed range size},\end{aligned}$$

$$\begin{aligned}&\text{False presence rate}\\&=(\text{Modeled range size}-\text{Common range size})\\&\quad/\text{Observed range size},\end{aligned}$$

$$\begin{aligned}&\text{False absence rate}\\&=(\text{Observed range size}-\text{Common range size})\\&\quad/\text{Observed range size},\end{aligned}$$

where common range size represents the size of both observed and GCM/RCM-based model predicted common range. The relative range size compares the predicted range size of the GCM- or RCM-based model with that of the observed range size. The range overlapping rate measures the degree of overlap of the GCM- or RCM-based model with the observed range size. The false presence rate is a measure of model over-prediction (error of commission) and the false absence rate is a measure of under-prediction (error of omission). In our analysis, an ideal prediction would have relative range size = 1, range overlapping rate = 1, false presence rate = 0, and false absence rate = 0.

Two indices are used to quantify future changes in species distributions. The first one is relative range size change (relative range size- 1), using the numerator as the predictor for future conditions, and the denominator for current conditions. The other one is "turnover," which measures the distributional shifts by areas the species' habitat loses or gains (Thuiller, 2004):

$$\text{Turnover} = 100 \times (S_{\text{gain}} + S_{\text{lost}})/(S_{\text{current}} + S_{\text{gain}}).$$

3 Results

The selected 13 invasive species (Table 1) across the U.S. have contrasting spatial pattern characteristics so as to test effects of input bioclimatic variables on model performance across a range of distribution types (Fig. 2). Based on available location data, samples of Yellow toadflax, Buffelgrass, and Brazilian pepper-tree are restricted to Colorado, southern Arizona, and Florida, respectively. Their sample sizes are relatively small (less than 100, Table 1). Bull thistle, Dalmatian toadflax, and Russian olive are present mainly over the western U.S. intermountain areas, while Musk thistle and Bindweed are sparsely distributed across the conterminous U.S. except in the south. These five species have a sample size between 100 and 200. Russian thistle has 205 samples but appeared in Arizona and Colorado only in the available dataset. In contrast, Canada thistle (265 samples) is distributed over a broader area in the northern U.S., and Cheatgrass and Japanese honeysuckle have abundant presence samples (534 and 562) and show a concentrated distribution over the southwestern and southeastern U.S., respectively. The largest sample size is 987 for tamarisk, which is distributed over large areas of the western U.S.

3.1 Accuracy assessment for species distribution models

The accuracy of the statistically fitted species distribution models by Maxent for each species were first assessed by measuring the consistency between the simulated present-day distributions based on weather station data and the test dataset using the AUC score (Table 1). The results show overall very good ability to predict the observed species presence points, with AUC values ranging from 0.83 (Tamarisk) to as high as 0.98 (Brazilian pepper-tree and Yellow toadflax). Nine of the 13 species have excellent accuracy ($\text{AUC} > 0.9$), and the other four species have good accuracy ($0.8 < \text{AUC} \leqslant 0.9$).

Sample size and species range impact AUC, such that small sample sizes and narrow ranges tend to produce high AUCs (Phillips, 2005). For example, Yellow toadflax, with the highest AUC (0.98), has the smallest sample size and narrowest range; Tamarisk has the most abundant sample points distributed over a broad area, and it also has the lowest AUC. Presence samples of Canada thistle are distributed sparsely over a very large area resulting in a lower AUC, compared to the concentration of Japanese honeysuckle samples. However, Canada thistle had a smaller sample size than Japanese honeysuckle (262 vs. 562), but the thistle model had a lower AUC.

A reference condition for the potentially suitable habitat of a species can be modeled using observed weather stations and current species locations (Fig. 3). Consistent with the available data used here, and sample distributions (Fig. 2), the models successfully depict climatically suitable habitats for each species. Brazilian pepper-tree is restricted to Florida, Buffelgrass is distributed over the southwest, and Japanese honeysuckle occupies the areas from the Northeast to the Midwest. The other 10 species show similar distributions over the eastern mountainous areas, although Canada thistle, Cheatgrass, Musk thistle, and Russian olive also have patches over the Northeast and land around the Great Lakes. The modeled habitat suitability for each species was used to evaluate how GCM-based and RCM-based inputs affected predictions of habitat suitability.

3.2 Current presence probability distribution

Based on the obvious uncertainty of future climate scenarios, the credibility of future species distribution predictions by GCM- or RCM-based models can only be evaluated through determining their ability to reproduce reference distributions based on weather station data and current distributions. Consider the species' habitat suitability based on GCM model inputs (Fig. 4). Among all of the 13 species, only the distribution of Brazilian pepper-tree showed any consistency between current observations and the reference models. However, even Brazilian pepper-tree extended far beyond its current locations, well along the southern and eastern coasts. For the other species, the GCM-based models markedly shrunk or expanded, and shifted suitable habitat, showing little similarity with the reference results (Fig. 3). Only sporadically were areas with very low probability ($< 30\%$ probability) reproduced by GCM-based models for Yellow toadflax, Buffelgrass, Dalmatian toadflax, Russian thistle, Cheatgrass, Japanese honeysuckle, and Tamarisk (Fig. 4). For the other five species (Bull thistle, Russian olive, Musk thistle, Bindweed, and Canada thistle), the GCM-based models produced much larger and misplaced areas of suitable

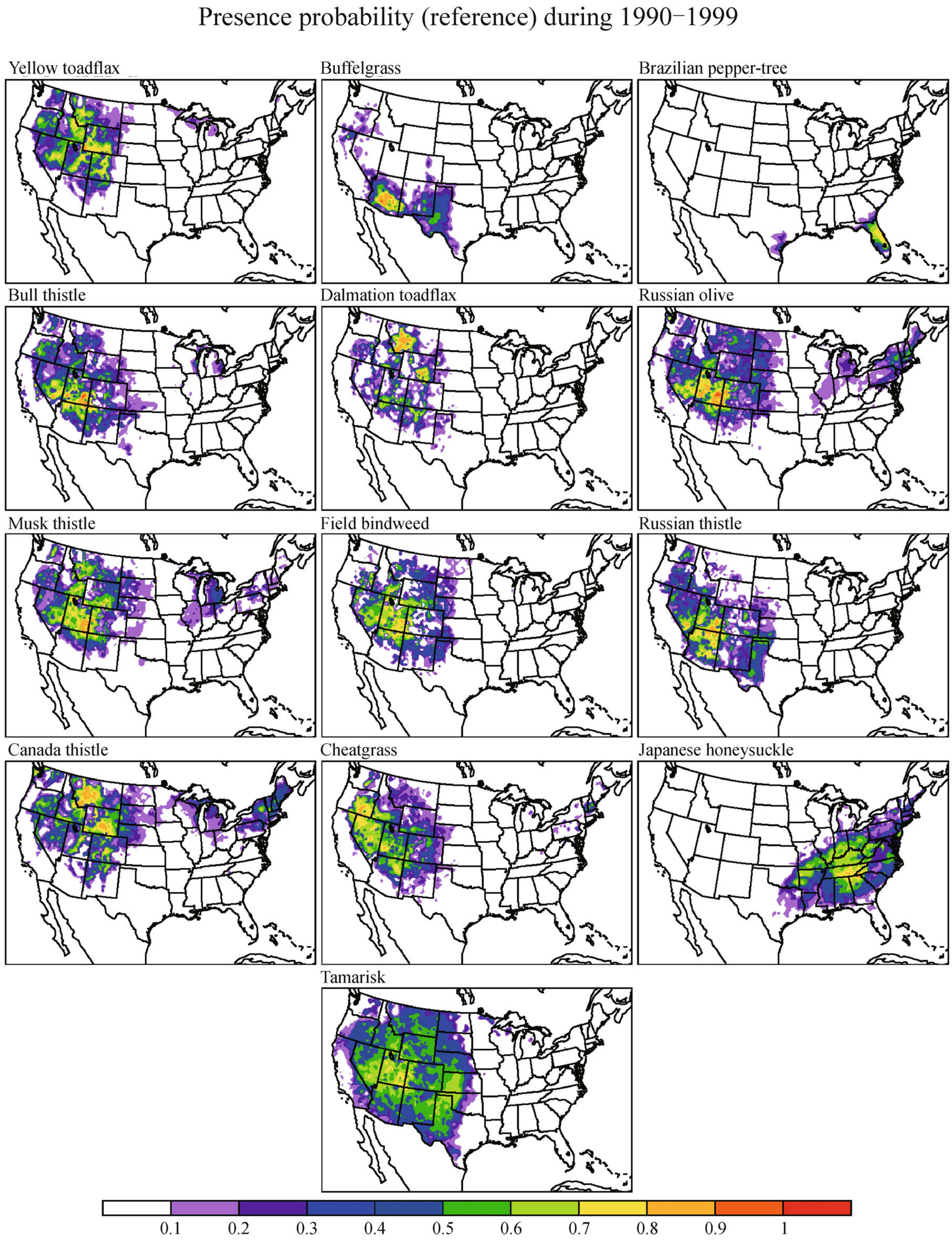

Fig. 3 Presence probability distribution predicted by species distribution models driven by observed bioclimatic variables (reference).

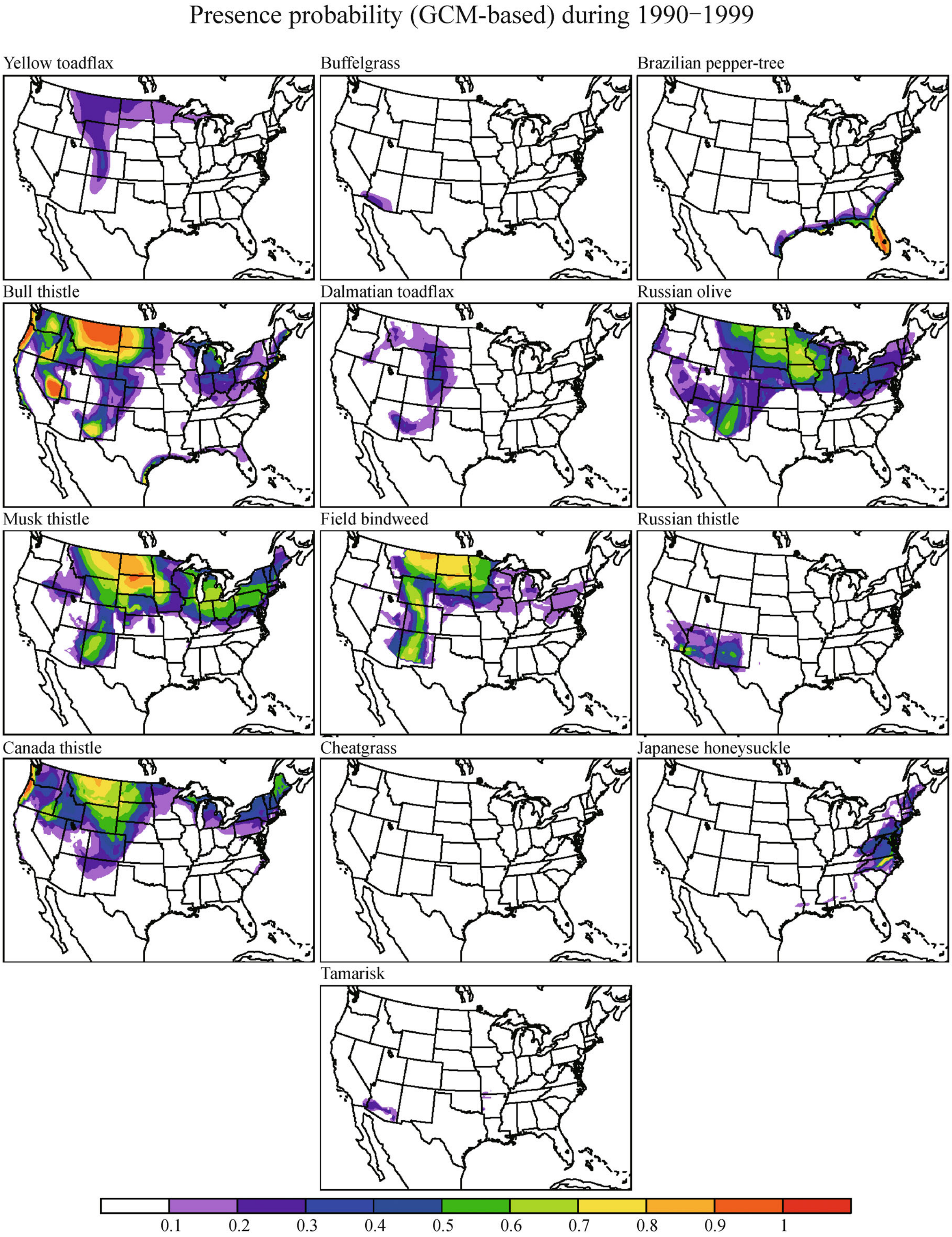

Fig. 4 Presence probability distributions predicted by species distribution models driven by the general circulation model simulated bioclimatic variables (GCM-based).

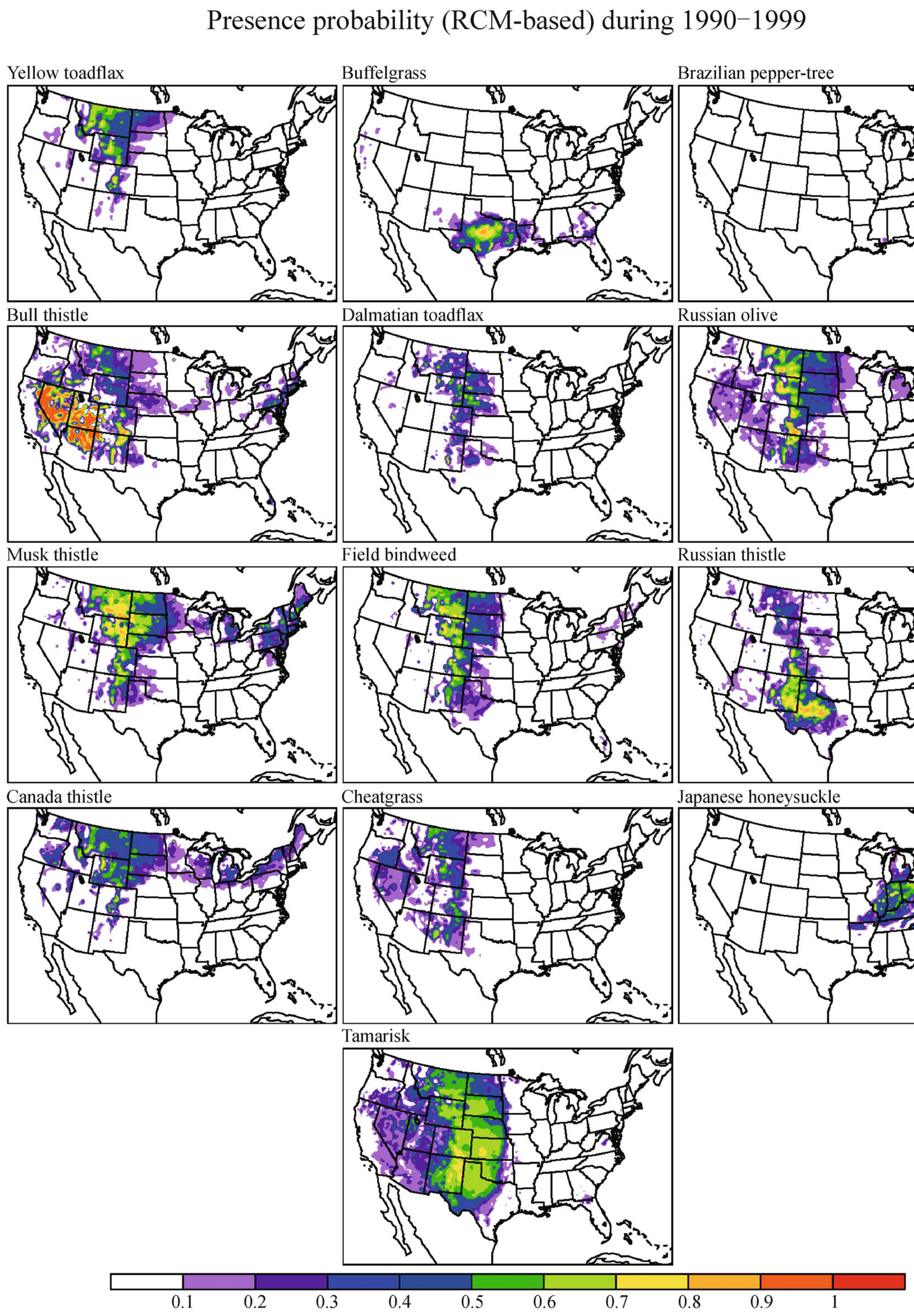

Fig. 5 Presence probability distributions predicted by species distribution models driven by regional climate model downscaled bioclimatic variables (RCM-based).

habitat compared to reference conditions (Fig. 4 vs. Fig. 3).

Now consider the habitat suitability maps generated with RCM-based inputs (Fig. 5). Compared to the GCM-based model results the RCM-based models produced far more similar patterns to the reference models (Fig. 5 vs. Fig. 3). For the seven species (Yellow toadflax, buffelgrass, Dalmatian toadflax, Russian thistle, Cheatgrass, Japanese honeysuckle, and Tamarisk) whose presences were unduly limited according to the GCM-based models (Fig. 4), the RCM-based models generally showed larger ranges, especially for Tamarisk. For the other five species (Bull thistle, Russian olive, Musk thistle, Bindweed, and Canada thistle) which were widely distributed across the U.S. according to the GCM-based models, the RCM-based models more closely simulated the available location data for the species (Fig. 2). Thus, the GCM-based model was more similar to the reference distribution (Fig. 3) for only one of thirteen species that were tested, Brazilian pepper-tree. Though certain similarities exist between GCM- and RCM-based models for Yellow toadflax and Canada thistle, the maps for the other species (especially Buffelgrass, cheatgrass, Russian thistle, and Tamarisk) have few areas in common between the two simulations (Fig. 4 vs. Fig. 5).

The dramatic effect of the different climatic dataset inputs on the species distribution models is further indicated by the statistical indices (Table 2). Presence thresholds differed wildly among the species, ranging from 0.1 (Brazilian pepper-tree) to 0.46 (Tamarisk). Based on these thresholds, the four indices of relative range size, range overlapping rate, false presence rate, and false absence rate also varied greatly between GCM- and RCM-based models, with a range size up to 18 times larger than reference models for Brazilian pepper-tree (Fig. 3). Other species, for which GCM-based models produced a larger range size than did reference models (i.e., relative range size > 1) included Bull thistle (8.5), Canada thistle (5.0), Bindweed (2.5), Musk thistle (2.7), and Russian olive (1.8). The relative range size values for two species (Cheatgrass and Tamarisk) are essentially zero, indicating that the GCM-based models do not generate any presence locations for these two species. The other five species had relative range size values < 1 with 0.41 as the largest value.

In contrast, RCM-based models have relative range size values between 0.5 and 6.4. The relative range size value = 1.0 for tamarisk, indicated that the range size was identical to the reference model (Fig. 3). Six other species (Yellow toadflax, Buffelgrass, Dalmatian toadflax, Russian olive, Musk thistle, and Bindweed) have reasonable relative range size values, around 1.3 to 1.7. The two species, Brazilian pepper-tree and Bull thistle, for which the RCM-based model produced large relative range size values (6.4, 5.1), had much greater values (8.5, 18.5) using the GCM-based models. For the remaining two species, Cheatgrass and Japanese honeysuckle, the RCM-based models produced lower relative range size values (0.5), while the GCM-based models produced worse results (0.0, 0.3). Clearly, the RCM-based models generally performed better than the GCM-based models. Note that for three species (Buffelgrass, Dalmatian toadflax, and Yellow toadflax), the GCM-based models under-predicted range size, but the RCM-based models over-predicted range size.

The range overlapping rate, the degree of overlap of the GCM- or the RCM-based models with the observed range size, varied greatly across the climate dataset inputs. For three of the species (Brazilian pepper-tree, Canada thistle,

Table 2 Statistical indices relative to reference during 1990–1999

Species	Presence threshold	Relative range size		Range overlapping rate		False presence rate		False absence rate	
		GCM	RCM	GCM	RCM	GCM	RCM	GCM	RCM
Yellow toadflax	0.36	0.30	1.32	0.00	0.19	0.30	1.13	1.00	0.81
Buffelgrass	0.20	0.09	1.38	0.04	0.21	0.06	1.17	0.96	0.79
Brazilian pepper-tree	0.10	18.46	5.08	**0.89**	**0.29**	17.57	4.80	0.11	0.71
Bull thistle	0.29	8.53	6.43	0.49	0.53	8.04	5.89	0.51	0.47
Dalmatian toadflax	0.27	0.41	1.29	0.02	0.12	0.39	1.17	0.98	0.88
Russian olive	0.32	1.82	1.43	0.18	0.26	1.65	1.17	0.82	0.74
Musk thistle	0.33	2.72	1.67	**0.38**	**0.25**	2.33	1.42	0.62	0.75
Canada thistle	0.35	4.96	4.24	**0.58**	**0.35**	4.38	3.89	0.42	0.65
Russian thistle	0.29	0.34	0.64	0.07	0.20	0.27	0.44	0.93	0.80
Bindweed	0.39	2.47	1.44	*0.15*	*0.14*	2.32	1.30	0.85	0.86
Cheatgrass	0.33	0.00	0.49	0.00	0.12	0.00	0.37	1.00	0.88
Japanese honeysuckle	0.36	0.26	0.49	0.08	0.24	0.18	0.24	0.92	0.76
Tamarisk	0.46	0.00	1.00	0.00	0.48	0.00	0.52	1.00	0.52

Note: Bold numbers indicate larger GCM-based model range overlapping rate values compared to RCM-based models. *Italic* numbers indicate close range overlapping rate values between the GCM-based and RCM-based models.

and Musk thistle), the GCM-based models produced higher range overlapping rate values than RCM-based models. Bindweed had similar values between the two. This may suggest better performance of the GCM-based models, except that higher range overlapping rate values were often accompanied by greater relative range size values, and large areas of false presences. All of the other nine species had greater range overlapping rates using RCM-based inputs. Note that three species (Cheatgrass, Tamarisk, and Yellow toadflax) had alarming zero values for range overlap rate, indicating that the models failed to reproduce the observed reference distributions for the species (Fig. 3).

3.3 Modeling future distributions of species

There are several statistical and ecological caveats to modeling future species distributions from incomplete data on present-day locations and uncertain climate change scenarios (Jarnevich and Stohlgren, 2009; and later in the Discussion). We focus attention here on statistical differences in future species distribution projections based on either GCM-based models or RCM-based models (Table 3). For example, the relative range size and turnover could not be calculated for Cheatgrass and Tamarisk using GCM-based scenarios, because neither species had a probability value greater than their presence threshold under the current climate. Both species are expected to extirpate from the U.S. Meanwhile, the RCM-based models predicted little change in range size of the same two species. GCM- and RCM-based models predicted same range change trend for five species: Yellow toadflax and Dalmatian toadflax are projected to shrink in the future; and Buffelgrass, Russian olive, and Russian thistle are projected to expand. The other six species have opposite signs of range size change between GCM- and RCM-based models with the former projecting expansion, except for Japanese honeysuckle.

Among the 11 species excluding Cheatgrass and Tamarisk, seven species (Brazilian pepper-tree, Bull thistle, Dalmatian toadflax, Russian olive, Musk thistle, Canada thistle, and Bindweed) project $< 10\%$ turnover difference value between GCM-based and RCM-based models, indicating little difference in the climate datasets used in projections (Table 3). The greatest difference in turnover was projected for Buffelgrass (50% turnover), with the GCM-based model projecting an 89% turnover, while the RCM-based model projected only 39%. Russian thistle also was projected to have high turnover.

We chose three species (Bull thistle, Canada thistle, and Tamarisk) for a comparison of the effects of climate dataset inputs on their projected species distributions under a fossil fuel intensive emission scenario. For Bull thistle, the GCM-based and RCM-based models produced similar results for range overlapping rate, range size change, and turnover (Table 3). Despite these statistical similarities, the spatial distributions were quite distinct, with the GCM-based distribution of Bull thistle projected in the northern U.S., while RCM-based model projections tended to be over the western Rocky Mountain area (Fig. 4 and Fig. 5).

For Canada thistle, GCM- and RCM-based models projected similar distribution patterns with the former having larger probability values (Fig. 4 and Fig. 5) resulting in greater range overlapping rate values (Table 2). As indicated earlier, the GCM-based model projected Tamarisk to be extirpated (i.e., extinct in the conterminous U.S.).

Both GCM- and RCM-based models projected dramatic changes in the distributions of bull thistle, Canada thistle, and Tamarisk in the future (Fig. 6). GCM-based models

Table 3 Statistical indices during 2046–2055 relative to 1990–1999 correspondingly

Species	Relative range size change		Turnover/%	
	GCM	RCM	GCM	RCM
Yellow toadflax	–0.4	–0.83	67.71	83.28
Buffelgrass	0.34	0.14	88.59	38.88
Brazilian pepper-tree	0.05	–0.14	53.97	54.72
Bull thistle	0.36	–0.09	36.54	33.54
Dalmatian toadflax	–0.5	–0.73	95.70	90.84
Russian olive	0.94	0.07	57.36	48.03
Musk thistle	1.00	–0.08	53.61	47.84
Canada thistle	0.37	–0.28	39.81	45.95
Russian thistle	1.33	0.95	86.08	59.35
Bindweed	0.02	–0.29	49.09	44.62
Cheatgrass	NaN	–0.1	NaN	58.28
Japanese honeysuckle	–0.24	0.26	92.87	71.24
Tamarisk	NaN	0.01	NaN	32.49

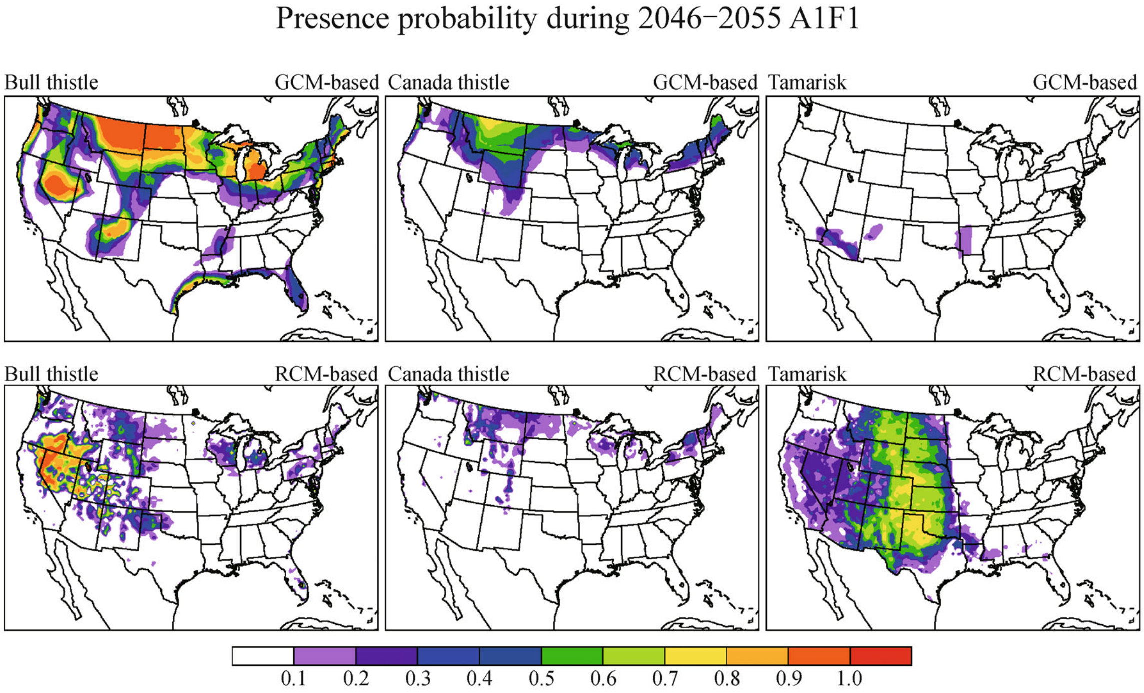

Fig. 6 Presence probability distribution for Bull thistle (left), Canada thistle (middle), and Tamarisk (right) predicted by GCM-based (upper) and RCM-based (lower) models during 2046–2055 under A1FI scenario.

projected bull thistle to occupy large areas in the north by expanding to the east around the Great Lakes, while RCM-based models projected reduced suitable habitats. Canada thistle was projected to center over Montana, with reduced suitable habitat using RCM-based inputs. Tamarisk all but disappeared using the GCM-based models, but remains widespread in the western U.S. if the models relied on RCM-based inputs.

4 Precipitation and surface air temperature

As shown, inputting different climate datasets into species distribution models can produce wildly different results for the same species. Since all six bioclimatic variables are derived from precipitation and surface air temperature, the resulting differences must come from the ability of GCM-based inputs or regional-climate based inputs in simulating these two variables. We compared observed, GCM simulated, and RCM downscaled temperature and precipitation results for 1990–1999 (Fig. 7). Observed precipitation showed distinct regional characteristics with a wet belt over the Cascades, dry areas over the Rocky Mountains, then increasing wetness from the West-Central U.S. to the East, and from north to south. GCMs fail to capture these important regional patterns, but they also produced dry biases over the Cascades and Southeast areas and wet biases over the Rocky Mountains. In contrast, the RCM substantially improved GCM results by generally reproducing observed precipitation patterns. Over the Southeast, however, the RCM simulations shifted the observed wet center north. The RCM also missed the high precipitation center in Florida.

Species whose distributions are strongly determined by precipitation patterns might be poorly modeled using GCM-based projections. For example, Tamarisk (Fig. 3) is generally restricted to xeric sites with < 1.2 mm/day precipitation. However, GCM-based models could not differentiate areas within this narrow precipitation range. Over-prediction of precipitation by the GCM in the areas where Tamarisk grows (Fig. 3) may limit its utility for mapping and predicting Tamarisk. RCM-based projections for Japanese honeysuckle (north-shift ranges in the Southeast) and Brazilian pepper-tree (limited presence in Florida) distributions (Fig. 5) also were associated with precipitation simulation deficiencies (Fig. 7). According to the Maxent models, Japanese honeysuckle requires > 2.8 mm/day precipitation and Brazilian pepper-tree is associated with between 1.3 mm/day and 2.9 mm/day precipitation.

For surface air temperature (Fig. 7), the GCM reproduced generally observed patterns, but missed the cold centers over the Rocky Mountains and regional-scale variability in all regions. The RCM accurately simulated the cold centers and the surrounding moderately cold areas. The GCM showed cold biases over the southern coast areas, while the RCM had warm biases. The spatial pattern correlation between the GCM and climate station observa-

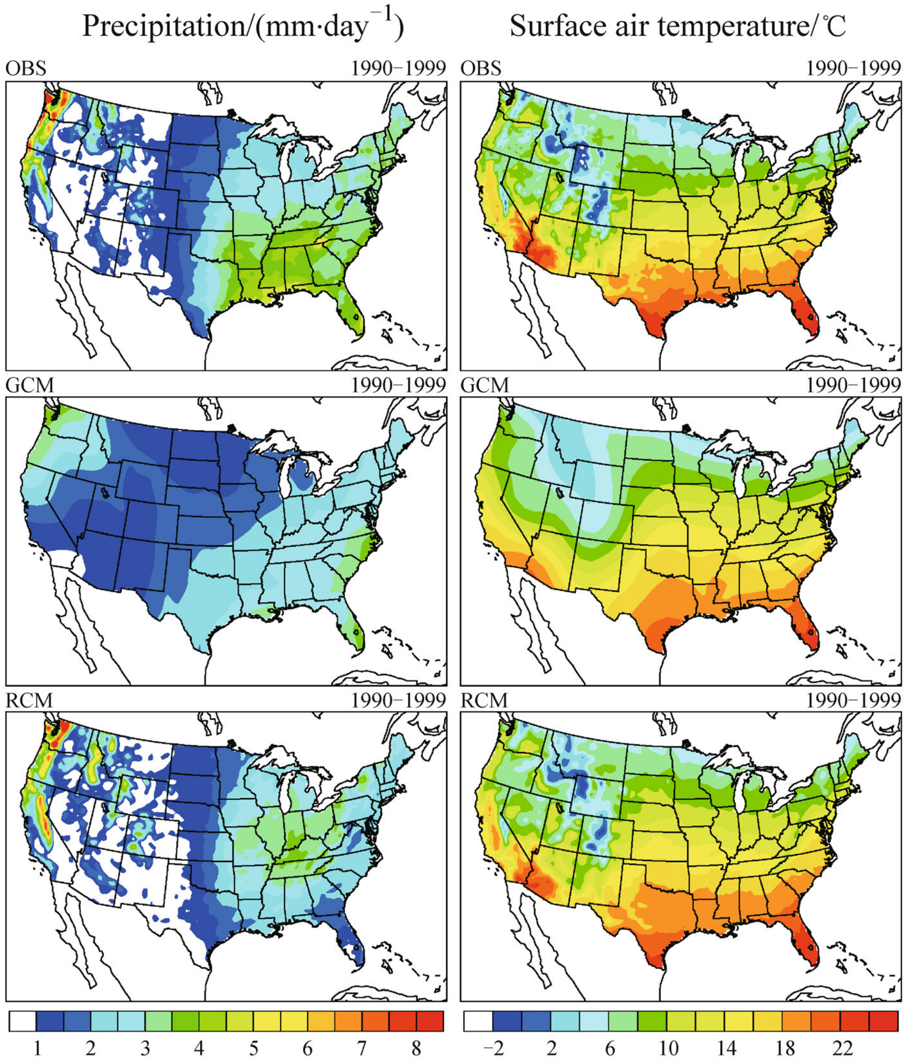

Fig. 7 Geographic distributions of annual mean precipitation (mm/day, left) and surface air temperature (C, right) during 1990–1999 as observed (OBS, upper), simulated by general circulation model (GCM, middle) and downscaled by regional climate model (RCM, lower)

tions was about 94%, while the RCM improved the correlation to over 98%. The root mean square errors were 1.9°C and 1.2°C for GCM and RCM, respectively. These statistical results showed that the RCM improved the GCM simulations. Bull thistle, Musk thistle, and Bindweed, whose distributions were adequately predicted by GCM-based models, were generally coincident with the northern cold areas. The species' high presence probability values (>0.7) were near Montana where the GCM projects a cold center. However, RCM-based models greatly improved the distributions for these species (especially Bull thistle) due to the realistic simulation of surface air temperature by the RCM (Fig. 5). According to the Maxent models, Bull thistle, Musk thistle, and Bindweed all grow in areas with annual mean surface air temperature $<$ 14°C. The broad cold surface air temperature distribution in the north simulated by the GCM contributed to these species' range shifts (Fig. 4).

5 Discussion and conclusions

This study demonstrated that species distribution models for 13 invasive plant species generally performed better when we used RCM-based inputs rather than whenGCM-based climate inputs (Table 2 and Table 3; Figs. 3–6) were used. The GCM-based models, particularly for Cheatgrass and Tamarisk, produced highly unrealistic results. Given our ecological understanding of Cheatgrass (Bromberg et al., 2011) and Tamarisk (Morisette et al., 2006, Jarnevich et al., 2011), it is highly unlikely these two species will be extirpated by changing climates any time soon.

George E.P. Box said, “All models are wrong, but some are useful." The space here does not allow for a full disclosure of caveats related to climate modeling and projections, and the caveats associated with modeling species distributions in space and time. Fortunately, the primary caveats for climate modeling have been covered

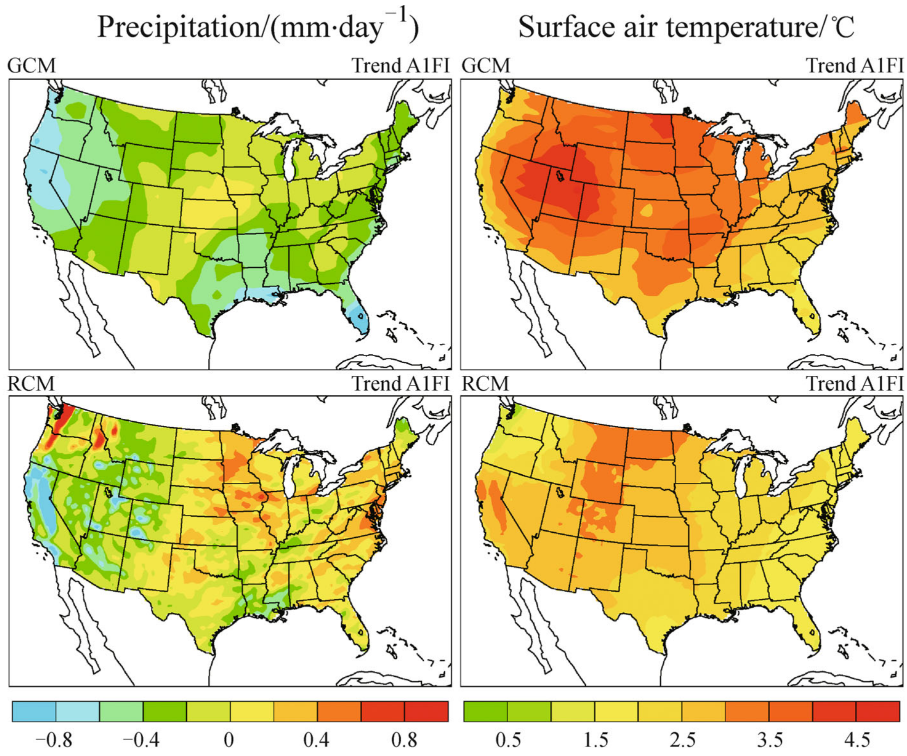

Fig. 8 Geographic distributions of annual mean precipitation (mm/day, left) and surface air temperature (C, right) trend during 2046–2055 under A1FI as simulated by the general circulation model (GCM, upper) and downscaled by regional climate model (RCM, lower).

by Tebaldi et al. (2005) and Pielke and Wilby (2012). Often cited caveats include a sparse and short climate record, currently unknown processes and interactions, and extremely limited means of evaluating uncertainty for projections in space and time. These issues cannot be dismissed. Instead, we view the process of ecological forecasting as a means to generate hypotheses.

Likewise, correlative species distribution models based solely on species presence and climatic factors at coarse scales (e.g., the 30 km×30 km scale used here; see Franklin et al., 2013) are only a first step in forecasting the effects of climate change on species distributions. While such models begin to elucidate a few fundamental species-environment relationships, reliable projections of range changes likely will only result from monitoring species abundance, persistence, dispersal, and migration, as well as soils, genetics, species interactions, and changes in disturbance regimes, land use, and trade and transportation, which continually bring in new invaders (Stohlgren et al., 2013). Still, when combined with a careful long-term monitoring program, preliminary species distribution models are essential for identifying potential leading and trailing edges of invasions, and the dominant environmental factors associated with species presence, abundance, and persistence.

We treat all model outputs as hypotheses to be tested in an iterative process of gathering new data, and validating, and improving models over time (Stohlgren and Schnase, 2006). Thus, we recognize that our "predictions" should be viewed as "possible outcomes", which are impossible to assess in terms of accuracy, precision, and uncertainty, except by waiting to see if the predictions hold true. However, some insights might be gained by evaluating the future projections against recent observed trends. For example, according to the GCM scenario used here (Fig. 8), most areas across the U.S. will become drier and hotter, with a warming center over the Rocky Mountains (up to 4.5°C). In contrast, the RCM predicts wetter conditions over only limited areas of the southwest coast and the Rocky Mountains. Opposite signs are produced by GCM (drier) and RCM (wetter) over the Cascades, eastern coast, and Gulf States. The RCM predicts < 3°C increase over most of the U.S., while GCM predictions often exceed 3°C.

Recent climate trends (after we conducted our analysis, but prior to publication), tend to support our less-extreme RCM scenarios compared to the more extreme GCM scenarios (Vose et al., 2012). While there is no way to verify the future species distributions projected by GCM- and RCM-based species distribution models (Fig. 6), there are several reasons that the less-extreme species distribution models from RCM scenarios may be viewed as "initially more credible." First, we know of no invasive species that have been extirpated from counties in the U.S. in the past decades (Stohlgren et al., 2008). Once established, invasive species tend to coexist with native species. Thus, the GCM-based projections of rapid extirpations of invasive species by 2055 (e.g., Cheatgrass and Tamarisk) may not be realistic. This may be especially true for cheatgrass which is facilitated by wildfire (Bromberg et al., 2011). Because turnover (Table 3) was projected to be less extreme with the RCM-based projections, and because observed climate changes are less extreme in accordance with recent observations (Vose et al., 2012, we suggest that RCM-based models may provide more credible future projections than GCM-based models.

Future research might wish to focus on the many interacting factors that play important roles in shaping species' future distributions at finer spatial scales (Pearson and Dawson, 2003). A better understanding of evolutionary change (Thomas et al., 2001), biotic interactions (Davis et al., 1998), and dispersal ability (Pearson and Dawson, 2003) is needed in order to develop species distribution modeling from purely deterministic, statistical models toward spatially explicit, process-based models (Davis et al., 1998; Root et al., 2003). A far better grasp is needed of uncertainty in space and time (Thuiller, 2004; Pearson et al., 2006; Liu et al., 2005). While species distribution models are primary tools for simulating the impact of climate change on species distributions, we are in our infancy in determining model accuracy and uncertainty (Pearson and Dawson, 2003; Araújo et al., 2005; Allouche et al., 2006).

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