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Climate Change May Alter Both Establishment and High Abundance of Red Brome (*Bromus rubens*) and African Mustard (*Brassica tournefortii*) in the Semiarid Southwest United States

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Nonnative, invasive plants are becoming increasingly widespread and abundant throughout the southwestern United States, leading to altered fire regimes and negative effects on native plant communities. Models of potential invasion are pertinent tools for informing regional management. However, most modeling studies have relied on occurrence data, which predict the potential for nonnative establishment only and can overestimate potential risk. We compiled locations of presence and high abundance for two problematic, invasive plants across the southwestern United States: red brome (*Bromus rubens* L.) and African mustard (*Brassica tournefortii* Gouan). Using an ensemble of five climate projections and two types of distribution model (MaxEnt and Bioclim), we modeled current and future climatic suitability for establishment of both species. We also used point locations of abundant infestations to model current and future climatic suitability for abundance (i.e., impact niche) of both species. Because interpretations of future ensemble models depend on the threshold used to delineate climatically suitable from unsuitable areas, we applied a low threshold (1 model of 10) and a high threshold (6 or more models of 10). Using the more-conservative high threshold, suitability for *Bromus rubens* presence expands by 12%, but high abundance contracts by 42%, whereas suitability for *Brassica tournefortii* presence and high abundance contract by 34% and 56%, respectively. Based on the low threshold (worst-case scenario), suitability for *Bromus rubens* presence and high abundance are projected to expand by 65% and 64%, respectively, whereas suitability for *Brassica tournefortii* presence and high abundance expand by 29% and 28%, respectively. The difference between results obtained from the high and low thresholds is indicative of the variability in climate models for this region but can serve as indicators of best- and worst-case scenarios.

Nomenclature: Red brome, *Bromus rubens* L.; African mustard, *Brassica tournefortii* Gouan.

Key words: Bioclimatic envelope modeling, ecological niche, fire regime, invasive plants.

The spread of nonnative, invasive plants can alter landscapes and degrade native ecosystem function (Mack et al. 2000). An invasive plant colonizes or is introduced to a novel location, establishes a self-sustaining population, and spreads into surrounding, uncolonized ecosystems (Lockwood et al. 2013; Richardson et al. 2000). Invasive plants can decrease species richness of native plants and animals (Vitousek et al. 1996), alter nutrient availability (Ehrenfeld 2003), and contribute to changes in disturbance regimes (Brooks et al. 2004). The recent, unprecedented increases in global temperature and changes in precipitation regimes predicted to occur during this century (Stocker et al. 2013) are likely to create novel environmental conditions and may increase opportunities for invasion by nonnative plant species (Bradley et al. 2010; Dukes and Mooney 1999). Spatially explicit invasion risk assessments (Peters and Lodge 2013; Rouget et al. 2002) could improve management by targeting high-risk areas for monitoring and control.

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Management Implications

In the arid and semiarid regions of the southwestern United States, two nonnative, invasive plant species, red brome (*Bromus rubens* L.) and African mustard (*Brassica tournefortii* Gouan) occur at varying levels of abundance. Within the study region (i.e., the area from which presence and high abundance data were collected), bioclimate envelope models (BEMs) indicate current widespread climatic suitability for the presence of both species. However, central and northwest Arizona, southern Nevada, and Baja California, Mexico, are currently most climatically suitable for high abundance of *Bromus rubens*. Hot, dry regions of southern California are currently most climatically suitable for high abundance of *Brassica tournefortii*. Based on a high threshold (6 or more of 10 models project suitability), climatic suitability is projected to increase only for *Bromus rubens* presence (+12%), whereas climatic suitability for *Brassica tournefortii* presence could decrease (−34%). Similarly, climatic suitability for high abundance of *Bromus rubens* (−42%) and *Brassica tournefortii* (−56%) could also decrease. For *Brassica tournefortii*, areas of contraction (i.e., projected loss of climatic suitability) appear in southern Arizona and California, and in Baja California and Sonora, Mexico. For high abundance of *Bromus rubens*, contraction is projected to occur along the southern edges of climatically suitable area, primarily in Arizona and Nevada. Climatic suitability for *Brassica tournefortii* is projected to contract mainly in western Nevada, southeastern California, and Baja California, Mexico. Based on an ensemble of future models and a low threshold (any 1 of 10 models projects suitability), climatic suitability for the presence of *Bromus rubens* and *Brassica tournefortii* could increase by up to 65% and 29%, respectively, by 2050. Climatic suitability for high abundance of *Bromus rubens* could expand northward into Nevada and Utah by up to 64%, indicating that these areas might be at an elevated risk for impact from this species in the future. Area suitable for *Brassica tournefortii* high abundance could expand by up to 28% by 2050 with slight increases in suitable area projected in southern Nevada, California, and Arizona. Efforts to minimize the impact of *Bromus rubens* and *Brassica tournefortii* would be more effective if focused on the areas identified as suitable for high abundance (rather than suitable for presence only) and likely to maintain or expand climatic habitat according to multiple projections.

The greatest potential damage to an ecosystem occurs not only where a nonnative species can establish but also where it can spread and become abundant (Parker et al. 1999). Populations of species occur at varying levels of abundance across landscapes, influenced by biotic and abiotic conditions (Brown 1995). Areas where invasive plants reach high abundance have the greatest probability of detrimental ecosystem effects (Brooks et al. 2004; Parker et al. 1999). For example, in the arid and semiarid ecosystems that characterize the southwestern United States, isolated occurrences of invasive annual grasses, such as red brome (*Bromus rubens* L.), are unlikely to cause significant damage. However, high abundance of these plants can reduce native plant biomass (Brooks 2000) and increase fire frequency (Balch et al. 2013) because of continuous cover of fine fuels (Brooks 1999; D'Antonio and Vitousek 1992). Forecasting invasive plant abundance will increase our ability to manage regional invasions in a changing climate by identifying emerging areas of high risk for monitoring and control.

Bioclimatic envelope models (BEMs) have become an increasingly common tool for quantifying the relationship between occurrences of a species and regional-scale climate conditions. BEMs are used to estimate the geographic range of climatic suitability and to understand how that range might shift as climate changes. However, although abundance is arguably more important for prioritizing management, most BEM studies have modeled suitability for invasive plant presence only because of the scarcity of abundance information across broad regions (see for examples Bradley 2013). Unfortunately, models based on invasive plant presence vastly overestimate potential abundance and associated impact (Bradley 2013).

Previous studies have argued that modeling the "impact niche" (Leibold 1995) or "damage niche" (McDonald et al. 2009) associated with locations of high abundance gives more realistic information about environmental effects than does modeling occurrences alone. For example, McDonald et al. (2009) used surveys of weed experts to identify states where cropping systems were highly affected by velvetleaf (*Abutilon theophrasti* Medik.) or johnsongrass [*Sorghum halepense* (L.) Pers.] and modeled the impact niche under current and future climate, based on these high-impact locations. Similarly, Bradley (2013) used surveys of invasive plant managers to identify locations with high invasive plant abundance to model the impact niche. In the absence of regional, continuous cover data (which are exceedingly rare for any species), point locations of high abundance can be used to model climatic conditions that describe the impact niche (Bradley 2013; Estes et al. 2013; McDonald et al. 2009), a subset of the total potential range.

Here, we used BEMs to project the current and potential future distributions of two of the most common and problematic, invasive species in the southwestern United States: *Bromus rubens* and African mustard (*Brassica tournefortii* Gouan.). *Bromus rubens* is an invasive, annual grass, native to southern Europe, which was first recorded in the United States in the 1880s (Salo 2005). High abundance of *Bromus rubens* is most likely to occur following average or above-average winter rainfall (Brooks 2000). When growing in high abundance, *Bromus rubens* is able to dominate available water and nitrogen (Brooks 2000) and reduce native plant biomass (Brooks 2000; Salo 2005).

Brassica tournefortii is an annual forb, native to the semiarid and arid regions of northern Africa and to the Mediterranean regions of southern Europe, and was first collected in the United States in 1927 (Minnich and Sanders 2000). *Brassica tournefortii* produces prolific seeds that germinate when conditions are favorable (Bangle et al. 2008). Following periods of high precipitation, *Brassica tournefortii* populations reach higher abundances than they do in years with low or average precipitation (Minnich and Sanders 2000). *Brassica tournefortii* seeds germinate earlier than seeds of native species, and plants can grow and monopolize resources before native species emerge (Minnich and Sanders 2000).

Invasion of both *Bromus rubens* and *Brassica tournefortii* is a concern because of alteration to regional fire cycles. Historically, large-scale fires in the desert regions of the southwestern United States were infrequent because of the scarcity of fine fuels and the patchy native vegetation cover (Brooks and Pyke 2001). The addition of nonnative annuals increases aboveground biomass and the continuity of fine fuels among native plants (Brooks 1999). Invasions of alien species that produce prolific biomass lead to a "grass–fire cycle" that has been identified in many ecosystems globally (Brooks et al. 2004; D'Antonio and Vitousek 1992). In areas in which they reach high abundances, *Bromus rubens* and *Brassica tournefortii* have the potential to increase fire frequency.

BEMs based on all locations of species presence and BEMs based on the subset of high abundance points were created to separately model suitability for presence and suitability for high abundance. We applied the two BEMs to future climate-change scenarios based on five climate models to test how invasive species presence and high abundance are projected to change by 2050. Relative to current climate, we also identified locations of expanded risk (climatic suitability) of presence and high abundance.

Materials and Methods

Presence and High Abundance Data. Presence data for *Bromus rubens* and *Brassica tournefortii* were compiled from regional data sets (CalFlora; http://www.calflora.org/ and Cal-IPC http://www.cal-ipc.org/), surveys by managers with the Bureau of Land Management and the Mojave Desert Network Parks, records from local and regional biologists, and herbaria. These existing datasets were supplemented with two field surveys focused on roadsides only in southern Nevada, southern California, and Arizona (Appendix 1; http://dx.doi.org/10.1614/IPSM-D-14-00040.S1). For both species, some abundance data were available from land managers and herbarium records as values of percent cover and from field surveys as qualitative descriptions of relative abundance at each site. Abundance data tended to be collected within more-restricted areas where each species is problematic and, therefore, are likely representative of climatic conditions in heavily invaded landscapes.

We transformed these data into two groups for each species: presence and high abundance. We classified locations as high abundance if the species had at least 10% cover, if the area was described qualitatively as having continuous ground cover (categorical rank data), or if the target species was observed in abundance (percent cover or rank data) beyond the road corridor. We included all available presence data, including points with high abundance, in the presence data sets. Records for both species were restricted to the southwestern United States (i.e., the region from which *Bromus rubens* and *Brassica tournefortii* are problematic invaders). Therefore, we limited the extents of our study regions using a convex hull around the presence locations of each species. Absence data comparable in extent to the presence/high-abundance data were not available for either species. To remove duplicate entries and reduce sampling bias, we resampled each of the four data sets to include only one point per 2.5 arcmin climate-grid cell (see below). If more than one point within a grid cell had abundance data, we assumed that the grid cell was climatically suitable for the highest level of abundance, and the maximum abundance value was retained.

Even if comprehensively collected, invasive species distribution data might still underestimate climatic suitability because the species has not yet spread to the full range it could potentially invade (Araújo and Pearson 2005). High abundance points might further underestimate climatic suitability for abundance because species are less abundant following dry growing season conditions (Abatzoglou and Kolden 2011). Nonetheless, numerous studies have used an envelope-modeling approach to estimate potential range for invasive plants with the assumption that the distribution data reasonably approximate the climatic space in which the species could establish or become abundant (see for examples, Bradley 2013). The data compiled for this analysis extend across broad climatic gradients of the southwest region and, therefore, encompass a high proportion of available climate space, making this analysis consistent with other envelope-modeling studies. However, incomplete data could still lead to an underestimation of potential range for presence, high abundance, or both. Our results are also limited by the spatial extent of our models. To improve model performance, we limited the models to the area enclosed by the presence locations of each species. It is possible that current or future climatic suitability could extend beyond these boundaries and allow the distributions of *Bromus rubens* and *Brassica tournefortii* to expand further than what we have shown. Therefore, these and all envelope models should be interpreted as having fairly high confidence that areas modeled at risk are indeed at risk, but lower confidence that areas modeled as not at risk are indeed not.

Climate Data. We obtained data representing global current and projected future climate from WorldClim (http://www.worldclim.org/) as interpolated climate surface layers of mean monthly temperature and precipitation at 2.5-min spatial resolution. Current climate data for the period of 1950 to 2000 are available through WordClim as interpolated layers of monthly averages of mean, minimum, and maximum monthly temperature and mean monthly precipitation (Hijmans et al. 2005).

We used future climate projections from five atmosphere–ocean general circulation models (AOGCMs) from the Fifth Intergovernmental Panel on Climate Change (IPCC) report that were downscaled using the WorldClim 1.4 current climate data as a baseline (Hijmans et al. 2005). We chose climate-model projections based on those that predicted Pacific Northwest temperature and precipitation with the lowest error (Rupp et al. 2013). We assumed that this accuracy also held for the southwest because no comparable assessment for the southwest region is currently available. We selected AOGCMs based on their performance as assessed by Rupp et al. (2013) and availability of relative concentration pathways (RCPs) in WorldClim. In the Fifth IPCC assessment report, RCPs replace the previously used emissions scenarios (Nakicenovic and Swart 2000). We included AOGCM projections based on RCP4.5 and RCP8.5. RCP4.5 is the "medium-low" pathway in the Fifth IPCC report and is characterized by a stabilization of radiative forcing at 4.2 W m^{-2} by 2100, which corresponds to atmospheric CO_2 concentrations of 650 ppmv. RCP8.5 is the "high" pathway and projects a stabilization of radiative forcing at 8.3 W m^{-2} by 2100, which corresponds to atmospheric CO_2 concentrations of 900 ppmv (Stocker et al. 2013). Climate projections were based on five AOGCMs from the following modeling groups: National Center of Atmospheric Research, National Centre of Meteorological Research, Met Office Hadley Center, Atmosphere and Ocean Research Institute, National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology, and Norwegian Climate Center.

We used four climate-variable predictors derived from the climate data: mean monthly temperature for the coldest (January) and warmest (July) months of the year and accumulated precipitation for two quarters (March, April, May; and June, July, August). Precipitation for the winter quarter (December, January, February) and fall quarter (September, October, November) were not included because they were highly correlated with other precipitation predictors within the study region and were the least-important precipitation variables in MaxEnt models. These predictors were selected to encompass climatic conditions that likely influence both native and invasive species growth and reproduction. The timing and relative importance of climatic conditions that facilitate *Brassica tournefortii* growth are largely untested. *Bromus rubens* is thought to be limited by winter temperatures (Bykova and Sage 2012) and fall precipitation (Beatley 1966; Salo 2004). Both species likely interact with native perennial species that respond to spring and summer (monsoonal) precipitation. By using climate data that covered the range of seasonal climate conditions in the study regions, we allow the model fit to define climate conditions that influence species distribution and high abundance.

Modeling Presence and Abundance under Current Climate Conditions. Many techniques for BEM (also referred to as *species-distribution modeling*, *habitat-suitability modeling*, or *environmental-niche modeling*) have been developed. BEMs are used to understand the relationship between the geographic location where species occur and the climatic conditions at those locations (Franklin 2009). A model of suitable climate can then be projected back into geographic space to identify the spatial extents of the potential for invasive plant establishment or abundance. Suitable climate conditions can also be projected spatially based on the geographic distribution of future climate associated with climate change. For *Bromus rubens* and *Brassica tournefortii*, we used two BEM methods (MaxEnt and Bioclim) to predict the current and future geographic distributions of presence and high abundance.

We used MaxEnt (Version 3.3.3k), an implementation of maximum entropy modeling (Phillips et al. 2006), to model climatic suitability for the two coverage groups: presence and high abundance. MaxEnt relies on presence-only data, but generates pseudoabsences drawn from the study area to construct probabilistic relationships between climate and species distribution. Pseudoabsence points drawn from too far afield from occurrences can lead to underestimates of climatic habitat, whereas pseudoabsences too close and not distinct from occurrences can lead to overestimates of climatic habitat (VanDerWal et al. 2009). To include climate conditions with enough difference from occurrences to define suitability, but also where the species' could plausibly have been introduced, we selected pseudoabsence points in MaxEnt within a convex hull around each species' occurrences. To account for uneven sampling of occurrence points (Kramer-Schadt et al. 2013), we included a bias file for each of the species based on the presence of National Parks and distance to roads. Each MaxEnt model was evaluated by performing a 10-fold cross-validation (the default setting) to evaluate model fit. MaxEnt creates a different function for each climatic predictor variable related to the suitability of climate conditions for species presence based on data for the locations in which the species has been detected. This process generates a spatial model with continuous values associated with climatic suitability for occurrence. We transformed this continuous model into a binary suitable/unsuitable map based on a threshold value that encompassed 95% of the location points. Using this threshold assumes that the species' status at almost all of the locations was correctly identified, which is consistent with a goal of broadly characterizing invasion risk.

To reduce potential bias introduced by using a single BEM, we also created Bioclim models of climatic suitability for *Bromus rubens* and *Brassica tournefortii*. Bioclim identifies thresholds for each climatic predictor that encompass the distribution data (Busby 1991; Pearson and Dawson 2003). We used ArcGIS 10.1 (ESRI, Redlands, CA 92373) to extract the values of the four climate variables to all the known locations and then calculated climatic limits that encompassed 95% of the distribution data set. This threshold was created by excluding the climate values associated with the upper and lower 2.5% of presence or high abundance points. We calculated Bioclim climatic suitability as areas identified as suitable by all four climate layers. The MaxEnt and Bioclim results were combined to quantify the spatial extent of climatic suitability in either model.

We evaluated MaxEnt model performance based on the area under the curve (AUC) values, which are widely applied to determine agreement between predicted species distributions and occurrence records (Fielding and Bell 1997; Pearson et al. 2006; Thuiller 2003). AUC values are based on the receiver operating curve (ROC), which plots the rate of true-positive predictions (sensitivity) against false-positive predictions (specificity) with values ranging from 0.5 (no better than random) to 1 (perfect model prediction). For all models, we also calculated true-skill statistic (TSS). TSS (Allouche et al. 2006) provides a measure of the accuracy of presence–absence predictions based on calculations of sensitivity (proportion of true positives) and specificity (proportion of true absences). Values range from +1 to −1, with zero indicating model performance no better than expected by chance. These statistics are typically used to evaluate the accuracy of land-cover maps not projected-suitability models. Therefore, TSS values typically used to define good map accuracy are not applicable to suitability modeling because BEM projections aim to model climatic suitability for invasion, not the current distribution of invasive species.

Modeling Presence and Abundance under Future Climate Conditions. After establishing the climate conditions suitable for *Bromus rubens* and *Brassica tournefortii* based on current climate, we projected those conditions onto future climate models using the same thresholds used to describe current climatic suitability. We repeated this process for the five AOGCM projections.

We created ensemble models of future presence and high abundance of *Bromus rubens* and *Brassica tournefortii* by summing all of the binary climatic suitability maps (i.e., those created by MaxEnt and Bioclim for each AOGCM) to create models ranging from zero (unsuitable in all models) to 10 (suitable in all models). Combining models of suitability made with multiple BEMs and AOGCMs (Araújo and New 2007) reduces the effect of any single model or scenario, and the degree of model overlap provides a measure of confidence associated with model agreement. For example, there is less uncertainty about the future climatic suitability for presence or high abundance of areas that are projected to be suitable by a greater number of AOGCMs (greater model agreement). We created separate ensemble models for the two relative concentration pathways.

To identify climatic suitability for invasion by *Bromus rubens* and *Brassica tournefortii* in the future, we created maps of range shift that show areas of future expansion, maintenance, and contraction. We simplified this analysis by considering any area projected to have suitable climate conditions currently by either MaxEnt or Bioclim as suitable. We created two sets of range shift maps by applying a low and a high threshold for identifying suitability. The low threshold provided a very liberal interpretation of the data in which areas projected to be suitable by any one of the 10 models in the ensemble were considered suitable. The high threshold provided a more-conservative interpretation in which suitable areas had to be projected as suitable by 6 or more of the 10 models in the ensemble. We compared current and future suitability to measure the spatial extent of projected contraction and the maintenance and expansion of invasion risk by 2050 within the study region defined for each species.

Results and Discussion

Distribution Data. The spatial locations of high abundance, low abundance, and presence with unknown abundance are shown in Figure 1. At the 2.5-arcmin resolution, we compiled 3,303 occurrences of *Bromus rubens* and 1,855 occurrences of *Brassica tournefortii*. Within these data sets, we identified 110 locations of highly abundant *Bromus rubens* and 218 locations of highly abundant *Brassica tournefortii*. Further information on the data sources is presented in Appendix 1 (http://dx.doi.org/10.1614/IPSM-D-14-00040.S1).

Current Climatic Suitability for Invasion. Current climatic suitability for *Bromus rubens* and *Brassica tournefortii* presence extends throughout the study region, consistent with known location points (Figure 2A). Suitable climate for *Bromus rubens* high abundance is currently limited to relatively small areas of southern California, Nevada, and Utah and a larger region of central and northwestern Arizona (Figure 2B). Suitable climate for *Brassica tournefortii* high abundance occurs primarily in southern California (Figure 1B). Based on the AUC statistic for MaxEnt models and on TSS for all models, the projected models performed better than expected by random chance (Table 1). The smaller suitable range for high abundance (relative to presence) for both species

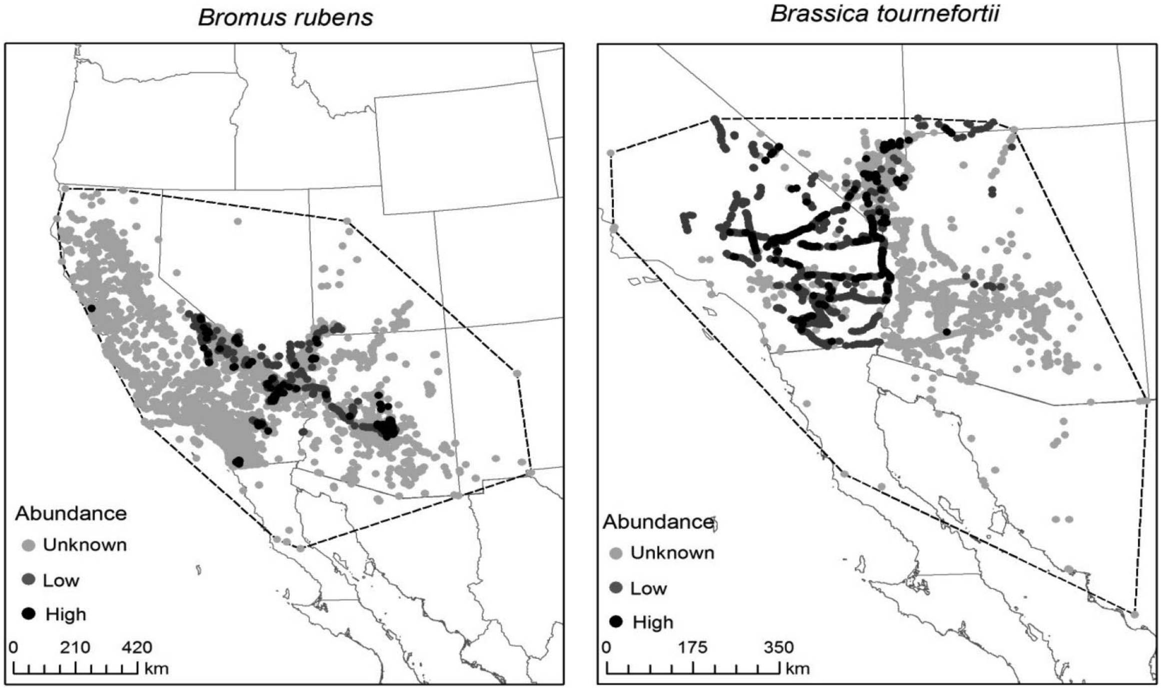

Figure 1. Spatial locations of data collection for each species. We classified locations as high abundance if the species was recorded as having at least 10% cover, if the area was described as having continuous ground cover, or if the species was observed in abundance beyond the road corridor. Points are shown as low abundance if they do not meet these criteria but have some description of abundance associated with them. Points lacking a description of abundance level are considered unknown. At the 2.5-arcmin resolution, we compiled 110 high-abundance occurrences for *Bromus rubens* and 218 for *Brassica tournefortii*; 243 points were classified as low abundance for *Bromus rubens* and 565 for *Brassica tournefortii*. Unknown abundance was found for 2,950 *Bromus rubens* points and 1,072 *Brassica tournefortii* points.

supports previous findings that models of potential establishment overestimate potential impact (Bradley 2013).

Based on the MaxEnt models, different climate conditions influence species presence vs. high abundance. For both *Bromus rubens* and *Brassica tournefortii*, temperature was by far the strongest predictor of presence (minimum temperature for *Bromus rubens* and maximum temperature for *Brassica tournefortii*). For *Bromus rubens*, this result suggests that freezing tolerance may limit the species' survival over winter, which is consistent with experimental studies (Bykova and Sage 2012). For *Brassica tournefortii*, this result suggests that the species effectively establishes under hot conditions, which is consistent with its measured heat tolerance (Suazo et al. 2012).

In contrast, minimum temperature and spring precipitation were both strong predictors of abundance for *Bromus rubens*, and summer precipitation was the strongest predictor of abundance for *Brassica tournefortii*. Both invasive species are likely to compete better against native species (e.g., Barrows et al. 2009) and have stronger population growth (Beatley 1974; Salo 2004) under wetter conditions. Thus, although temperatures limit the overall range, precipitation may be more influential on invader abundance.

Future Range Shifts with Climate Change. Projections of future climatic suitability for *Bromus rubens* and *Brassica tournefortii* presence and abundance under the RCP4.5 emissions pathway are shown in Figure 2C and 2D, respectively. The model projections based on RCP4.5 vs. RCP8.5 were similar both in overall magnitude of calculated range shift and spatial pattern. For simplicity, we present results from RCP4.5 in the main text and present the same results for RCP8.5 in Appendix 2 (http://dx.doi.org/10.1614/IPSM-D-14-00040.S1). An analysis of future climate conditions indicates that they are climatically similar to current conditions. That is, we are not extrapolating model fits into novel climate conditions (Appendix 3; http://dx.doi.org/10.1614/IPSM-D-14-00040.S1), which would increase uncertainty in model projections if it were the case.

Most models agreed that large areas will be suitable for *Bromus rubens* presence in the future (Figure 2C). Future suitability for *Bromus rubens* abundance is projected to be greatest in northwest Arizona, southwest Nevada, and Baja California, Mexico, based on ensemble model overlap

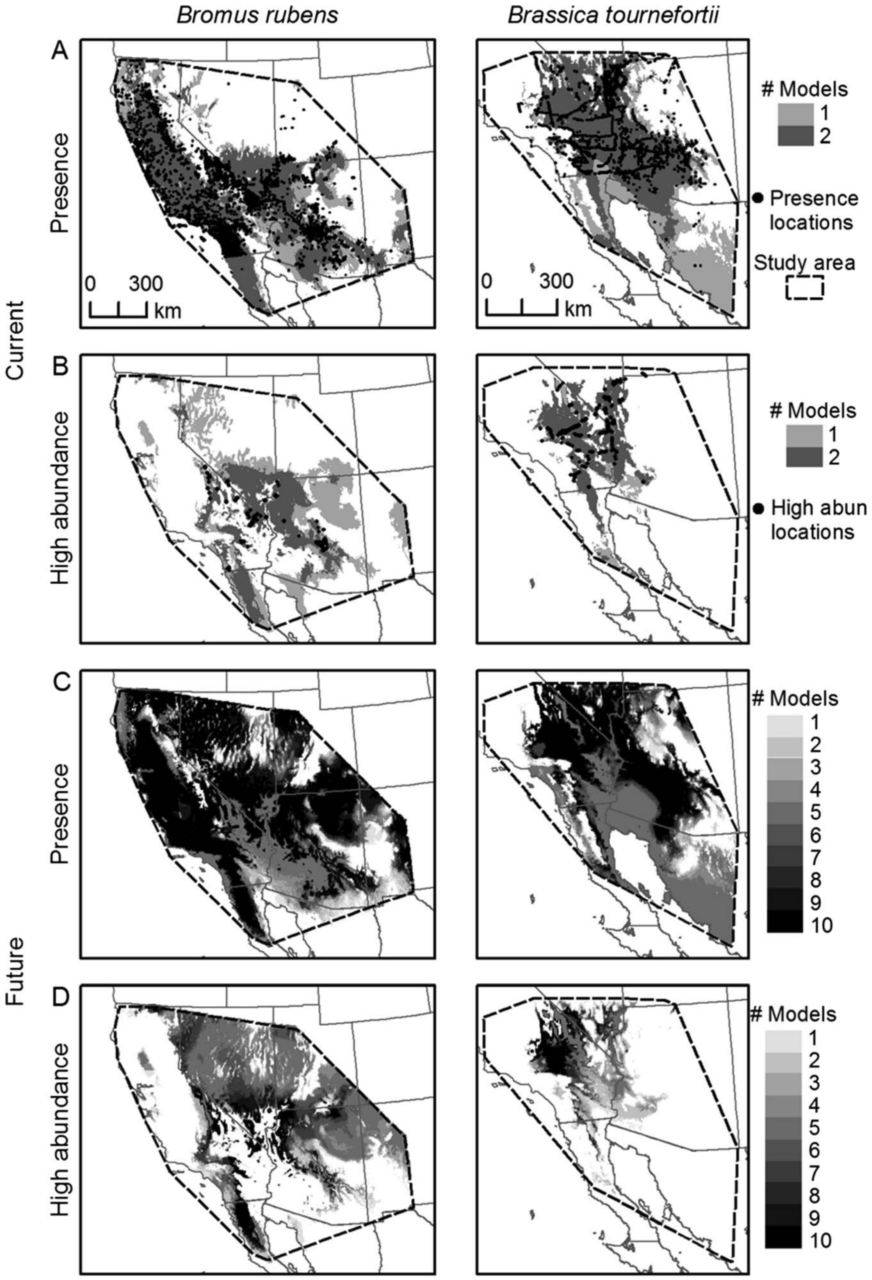

Figure 2. Species distribution models for *Bromus rubens* and *Brassica tournefortii*. Point locations indicate where (A) presence and (B) high abundance data were collected. The predicted current climatic suitability for (A) presence and (B) high abundance include the MaxEnt and Bioclim projections and encompass 95% of the original distribution data. Future ensemble models are based on RCP4.5. The future-ensemble models for (C) presence and (D) high abundance were created by combining the projections of 10 models: two bioclimate envelope models and five Atmosphere–Ocean General Circulation models. Values indicate how many of the 10 models projected climatic suitability.

(Figure 2D). Based on the high threshold (six or more models projecting suitability), climatic suitability for *Bromus rubens* presence could expand by 12% along the northern edge of the currently suitable range (Table 2; Figure 3A). However, contraction along the southern edge is also predicted, with areas primarily in Arizona becoming unsuitable. Using the more-inclusive low threshold (one or more models projecting suitability), climatic suitability for *Bromus rubens* presence could expand northward up to 65% (Figure 3B). In the model projections, northward expansion is primarily driven by warming temperatures, which is consistent with experimentally derived limitations.

Table 1. Model validation indicating agreement between the projected distribution and observations for each species for the current projections. Statistics were calculated for models based on presence data (P) and high-abundance data (HA). The true skill statistic (TSS) measures the map accuracy of presence–absence predictions and ranges in value from +1 to −1, with +1 indicating perfect model agreement and 0 indicating performance no better than expected by random chance. The area under the receiver operating curve (AUC) measures overall model accuracy and ranges from 0 to 1 with 0.5 indicating no better than random. AUC can only be calculated for models with continuous predictions of suitability (MaxEnt in this case).

	Bromus rubens		*Brassica tournefortii*		*Bromus rubens*		*Brassica tournefortii*	
	MaxEnt				Bioclim			
	P	HA	P	HA	P	HA	P	HA
TSS	0.50	0.76	0.39	0.75	0.54	0.66	0.56	0.79
Mean test AUC (SD)[a]	0.752 (0.008)	0.914 (0.037)	0.752 (0.020)	0.909 (0.017)	NA	NA	NA	NA

[a] Abbreviation: SD, standard deviation.

Bykova and Sage (2012) show that *Bromus rubens* is sensitive to freezing temperatures and is not as cold tolerant as the related species *Bromus tectorum.*

High abundance of *Bromus rubens* based on the high threshold could *decrease* by 42% (Table 2; Figure 3C). However, using the more-inclusive low threshold, climatic suitability for high abundance could expand northward by as much as 64% (Figure 3D). The large differences in potential future range illustrate uncertainty associated with both differences between BEMs and climate projections as well as the importance of choosing a threshold for delineating suitable from unsuitable. Areas of expansion in southern Nevada, northwestern Arizona, and Baja California, Mexico, show the highest model agreement (Figure 2). Therefore, these areas might see a shift toward high abundance of *Bromus rubens* with climate change. Interestingly, *Bromus rubens* is already present throughout southern Nevada, making it likely that populations will not be limited by propagules and could expand rapidly once climate conditions become suitable.

The future presence model of *Brassica tournefortii* shows high model agreement in southern California and Nevada and throughout much of Arizona (Figure 2C). Future climatic suitability for *Brassica tournefortii* is projected by most models to occur in southern California (Figure 2D). Based on the high threshold (six or more models projecting suitability), climate conditions suitable for *Brassica tournefortii* presence are projected to decrease by 34% overall, with areas in southern California, eastern Nevada, and Mexico becoming unsuitable (Table 2; Figure 3A). Using the more-inclusive low threshold (one or more models projecting suitability), climatic suitability for *Brassica tournefortii* could expand up to 29% (Figure 3B).

In contrast, climatic suitability for high abundance of *Brassica tournefortii* is projected to decrease by 56% (Table 2; Figure 3C). Using the inclusive low threshold, climatic suitability for high abundance expands by 28% (Figure 3D). The difference between these two projections can primarily be attributed to how MaxEnt vs. Bioclim interpret high temperatures for *Brassica tournefortii* (Appendix 4; http://dx.

Table 2. Projected increases in distribution size (km^2 × 1,000) within the study areas based on the low (one or more model projecting climatic suitability) and high (six or more models projecting climatic suitability) thresholds under future climate conditions for RCP4.5

			Low threshold		High threshold	
			Area	% Change	Area	% Change
Bromus rubens	Presence	Current	736		736	
		Future	1219	65	826	12
	High abundance	Current	475		475	
		Future	780	64	273	−42
Brassica tournefortii	Presence	Current	410		410	
		Future	531	29	270	−34
	High abundance	Current	135		135	
		Future	173	28	59	−56

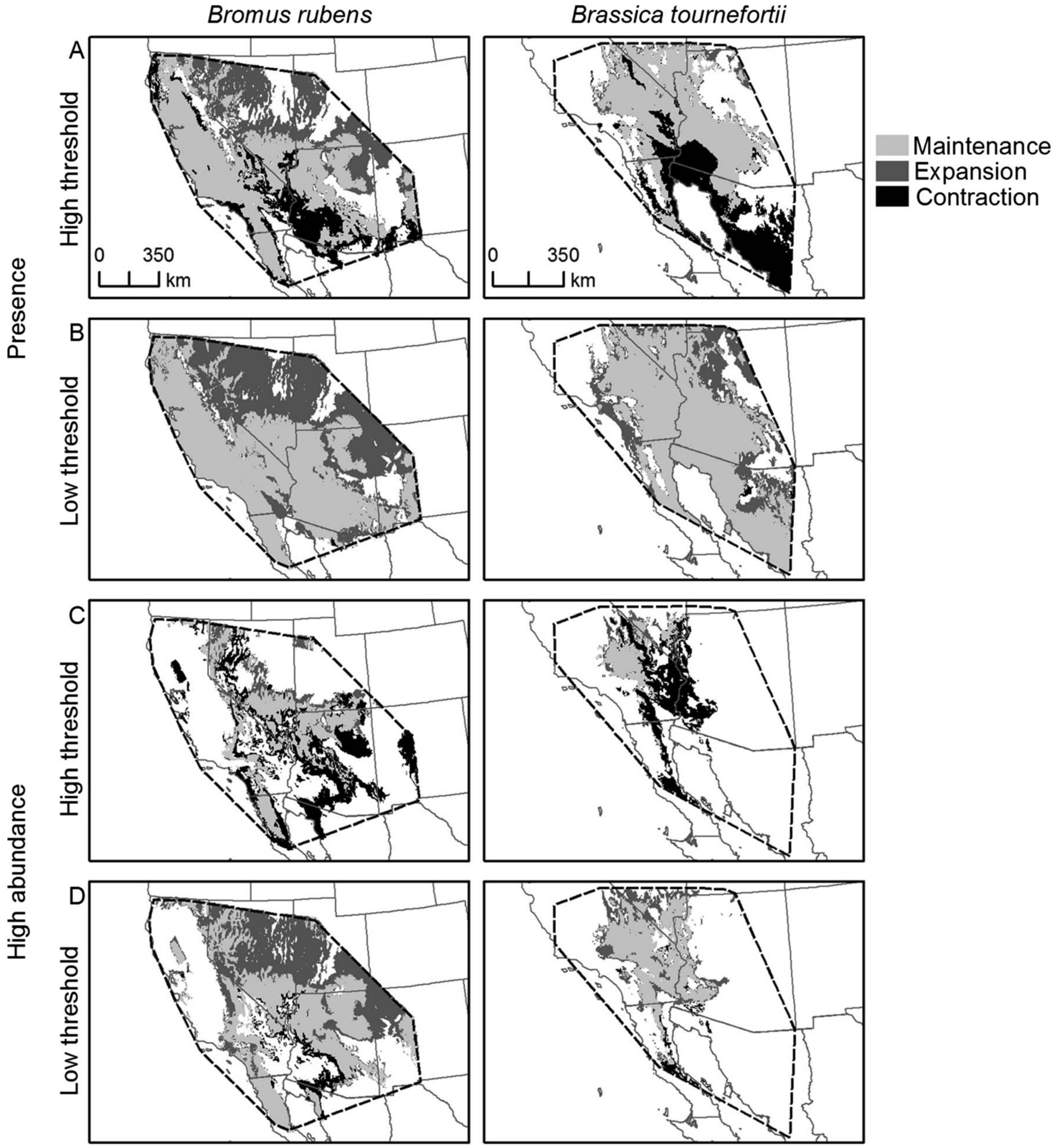

Figure 3. Distribution models showing maintenance, expansion, and contraction of suitable climate under future climate conditions for RCP4.5. Maintenance indicates that a location was climatically suitable both under current and future climate conditions. Expansion indicates that a location was climatically suitable under future, but not current climatic conditions. Contraction indicates that a location was climatically suitable under current, but not future climatic conditions. The high-threshold models (A and C) are based on a more conservative view of future climatic suitability, where six or more models must agree for a location to be included as future potential habitat. Low-threshold models (B and D) include all areas where at least one future model indicates suitable habitat.

doi.org/10.1614/IPSM-D-14-00040.S1). Bioclim identifies a high temperature threshold, above which conditions become unsuitable, whereas MaxEnt considers all high temperatures suitable. Although *Brassica tournefortii* has a broad tolerance for warm temperatures (Suazo et al. 2012), it is not clear whether it is approaching its high temperature limit within its current range. Further experimental analyses are required to enable better interpretation of the model results.

Suitable Area. Interpretations of future ensemble models strongly depend on how *suitable area* is differentiated from *unsuitable area*. The overall spatial extent of climatic suitability varies depending on the choice of an acceptable

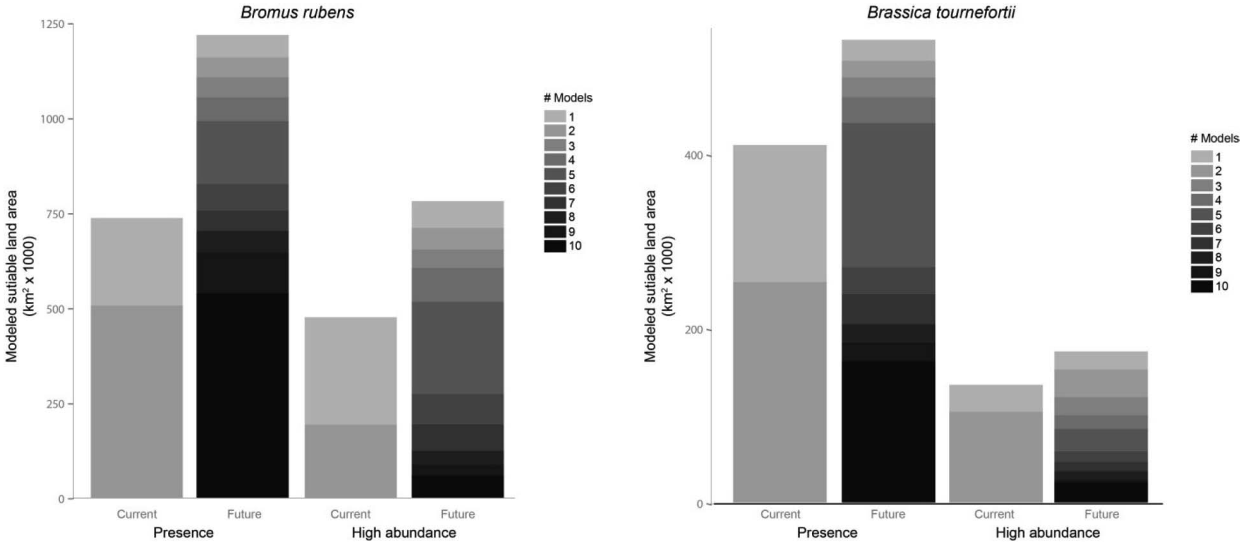

Figure 4. Predicted suitable land area for the target species currently and by 2050 under RCP4.5. Darker gray indicates higher ensemble model overlap.

threshold for identifying climatic suitability (Figure 4). Areas of high model overlap have less uncertainty. Despite differences in climate changes projected by these AOGCMs (Rupp et al. 2013), areas of high overlap maintain climatic suitability. For prioritizing management and control efforts, greater overlap is better than less overlap for identifying the most likely areas with future invasion risk (Figure 2). However, even areas with low overlap could still maintain or expand risk if undersampled distribution data cause models to underpredict climatic suitability. We suggest that locations of expansion, particularly using the high threshold (Figure 3A,C), are likely to be at the greatest risk, but contraction using the same high threshold may be overpredicted.

Conclusions

It is currently unknown whether the impact niche of invasive plants will respond to climate change in a similar direction and magnitude as the overall range. Based on the low threshold of model overlap, climatic suitability for presence and high abundance for *Bromus rubens* and *Brassica tournefortii* are projected to shift in a similar magnitude and direction under climate change. However, based on the high threshold of model overlap, climatic suitability for presence and high abundance are projected to vary considerably in magnitude and direction under climate change. Differences between shifts in modeled establishment niche and impact niche between the species highlight the need for considering both presence and high abundance in models of invasion risk. Overall, high abundance of nonnative, invasive plant species threatens native plant species and has the potential to alter ecosystem function (e.g., increased fire threat in areas with high abundance of *Bromus rubens* and *Brassica tournefortii*). Given the importance of understanding where the greatest threat is likely to occur, future analysis of range shifts for invasive plants should include suitability for high abundance where possible.

The relatively sparse amount of abundance data in this study highlights the need for a different focus in field data collection. Presence data are useful, but information on the relative abundance of invasive species, even qualitative information, is more directly related to their potential ecological effects (Bradley 2013; Leibold 1995; McDonald et al. 2009; Parker et al. 1999). Continuous cover data collected across broad climatic or latitudinal gradients would provide the most accurate representation of community composition at each location and would allow for more-comprehensive models of the response of species to climate change. In lieu of time-intensive continuous cover data, qualitative descriptions or cover ranks, such as those used here, can be used for identifying the impact niche of an invasive species.

Current models of the distributions of presence and abundance can be used to guide data collection by identifying areas projected to be climatically suitable but not previously sampled. They can also help to identify those regions with the greatest risk of impact from invasion, assuming that abundance and impact are positively correlated (Parker et al. 1999). Future research is needed to quantify whether and how abundance relates to impact, thereby enabling managers to use regional models to better target management action. Nonetheless, potential for an abundant infestation is likely to be of greater concern than potential for presence only and focusing management in areas with current and future climatic suitability for abundance is a good approach for mitigating future invasions.

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Literature Cited

Abatzoglou JT, Kolden CA (2011) Climate change in western us deserts: potential for increased wildfire and invasive annual grasses. Rangeland Ecol Manag 64:471–478

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47

Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. Ecography 28:693–695

Balch JK, Bradley BA, D'Antonio CM, Gómez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob Change Biol 19:173–183

Bangle DN, Walker LR, Powell EA (2008) Seed germination of the invasive plant *Brassica tournefortii* (Sahara mustard) in the Mojave Desert. West N Am Naturalist 68:334–342

Barrows CW, Allen EB, Brooks ML, Allen MF (2009) Effects of an invasive plant on a desert sand dune landscape. Biol Invasions 11: 673–686

Beatley JC (1966) Ecological status of introduced brome grasses (*Bromus* spp.) in desert vegetation of southern Nevada. Ecology 47:548–554

Beatley JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856–863

Bradley BA (2013) Distribution models of invasive plants over-estimate potential impact. Biol Invasions 15:1417–1429

Bradley BA, Wilcove DS, Oppenheimer M (2010) Climate change increases risk of plant invasion in the Eastern United States. Biol Invasions 12:1855–1872

Brooks ML (1999) Alien annual grasses and fire in the Mojave Desert. Madroño 46:13–19

Brooks ML (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. Am Midl Nat 144:92–108

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Brooks ML, Pyke DA (2001) Invasive plants and fire in the deserts of North America. Pages 1–14 *in* Galley KEM, Wilson TP, eds. Proceedings of the Invasive Species Workshop: The Role of Fire in the Spread and Control of Invasive Species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Tallahassee, FL: Tall Timbers Research Station Misc Pub 11

Brown JH (1995) Macroecology. Chicago: University of Chicago Press

Busby JR (1991) BIOCLIM—a bioclimate analysis and prediction system. Plant Prot Q 6:8–9

Bykova O, Sage RF (2012) Winter cold tolerance and the geographic range separation of *Bromus tectorum* and *Bromus rubens*, two severe invasive species in North America. Glob Change Biol 18:3654–3663

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends Ecol Evol 14:135–139

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523

Estes LD, Bradley BA, Beukes H, Hole DG, Lau M, Oppenheimer MG, Schulze R, Tadross MA, Turner WR (2013) Comparing mechanistic and empirical model projections of crop suitability and productivity: implications for ecological forecasting. Glob Ecol Biogeogr 22: 1007–1018

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Franklin J (2009) Mapping Species Distributions: Spatial Inference and Prediction. New York: Cambridge University Press

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. Divers Distrib 19:1366–1379

Leibold MA (1995) The Niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion Ecology. West Sussex, UK: Wiley-Blackwell

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

McDonald A, Riha S, DiTommaso A, DeGaetano A (2009) Climate change and the geography of weed damage: analysis of U.S. maize systems suggests the potential for significant range transformations. Agric Ecosyst Environ 130:131–140

Minnich R, Sanders A (2000) *Brassica tournefortii* Gouan. Pages 68–72 *in* Bossard C, Hoshovsky M, Randall J, eds. Invasive Plants of California's Wildlands. Berkeley, CA: University of California Press

Nakicenovic N, Swart R (2000) Special Report on Emissions Scenarios. Cambridge, England: Cambridge University Press

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Holle BV, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371

Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. J Biogeogr 33:1704–1711

Peters JA, Lodge DM (2013) Habitat, predation, and coexistence between invasive and native crayfishes: prioritizing lakes for invasion prevention. Biol Invasions 15:2489–2502

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib, 6:93–107

Rouget M, Richardson DM, Nel JL, Wilgen BWV (2002) Commercially important trees as invasive aliens—towards spatially explicit risk assessment at a national scale. Biol Invasions 4:397–412

Rupp DE, Abatzoglou JT, Hegewisch KC, Mote PW (2013) Evaluation of CMIP5 20th century climate simulations for the Pacific Northwest USA. J Geophys Res Atmos 118:10884–10906

Salo LF (2004) Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times for concern, opportunities for management. J Arid Environ 57:291–296

Salo LF (2005) Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. Biol Invasions 7:165–180

Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (2013) Climate Change 2013: The Physical Science Basis. Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5). New York: Cambridge University Press

Suazo AA, Spencer JE, Engel EC, Abella SR (2012) Responses of native and non-native Mojave Desert winter annuals to soil disturbance and water additions. Biol Invasions 14:215–227

Thuiller W (2003) BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. Glob Change Biol 9:1353–1362

VanDerWal J, Shoo LP, Graham C, Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecol Model 220:589–594

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:468–478

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