

# Predicting the Potential Distribution of Three Allergenic Invasive Ambrosia (Ragweed) Species in Asia

Z. Qin<sup>1</sup>, J. E. Zhang<sup>2\*</sup>, A. DiTommaso<sup>3</sup>, J. M. Diez<sup>4</sup>, Y. Zhao<sup>5</sup>, and F. G. Wang<sup>1</sup>

<sup>1</sup>The Department of Ecology, College of Natural Resources and Environment, South China Agricultural University, Guangzhou 510642, China

<sup>2</sup>Guangdong Province Key Laboratory of Eco-Circular Agriculture, South China Agricultural University, Guangzhou 510642, China

<sup>3</sup>Section of Soil and Crop Sciences, School of Integrative Plant Science, 903 Bradfield Hall, Cornell University, Ithaca, NY 14853, USA

<sup>4</sup>Department of Botany and Plant Sciences, University of California, Riverside, California 92521, USA

<sup>5</sup>School of Geography and Planning, Sun Yat-sen University, Guangzhou 510275, China

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**ABSTRACT.** Three ragweed species native to North America (*Ambrosia artemisiifolia* L., *A. psilostachya* DC, and *A. trifida* L.) that have been introduced into Asia are now spreading quickly in many regions. Predicting which specific areas may be vulnerable to the invasion of these allergenic *Ambrosia* species can provide valuable insights for early detection and for prioritizing preventive actions. Species distribution models, based on native and non-Asian occurrence records for these three *Ambrosia* species, were generated with the maximum entropy (Maxent) approach respectively. Spatial filtering and target-group background methods were used to address sampling bias. Models fitted with different levels of complexity under present conditions were compared and evaluated with independent Asian records. Models showing lower over-fitting and higher performance were then selected to assess their future distribution under two types of Representative Concentration Pathways (RCP4.5 and RCP8.5), using four General Circulation Models (GCMs). Predicted habitats for *A. artemisiifolia* in 2050 would contract in regions having been colonized, despite a limited increase in parts of China. This species may experience a southward range shift in China. Under all future climate scenarios, *A. trifida* was predicted to decrease its potential establishment while *A. psilostachya* would expand its range, especially in habitats being colonized currently. Special attention should be given to Hunan, Jiangxi Provinces and scattered along southeastern coastal regions of China as well as parts of Turkey and northwest Iran, Azerbaijan, considering that future potential distribution of *A. artemisiifolia* and *A. psilostachya* might increase in these areas respectively. The findings provide valuable information for assessing the risk that these three *Ambrosia* species pose to many Asian countries and for prioritizing early detection and prevention strategies.

**Keywords:** *Ambrosia artemisiifolia*, *A. psilostachya*, *A. trifida*, climate change, invasive species, Asia, Maxent, species distribution modeling

## 1. Introduction

There is growing evidence that anthropogenically-induced climate change and increasing atmospheric CO<sub>2</sub> concentrations have the potential to transform almost all spatial and temporal aspects of plant-based aeroallergens (production, allergenicity, and distribution), with subsequent effects on aeroallergen exposure and the severity of allergic diseases (Hickler et al., 2012; Ziska and Beggs, 2012). Among the most troublesome and abundant allergenic plants are ragweed (*Ambrosia*) species that can severely impact public health via highly allergenic pollen (Oswalt and Marshall, 2008; Smith et al., 2013). In Asia, three species of ragweed have been recorded: *Ambrosia artemisiifolia* L. (Common ragweed), *A. psilostachya* DC. (Perennial ragweed) and *A. trifida* L. (Giant ragweed). All three species are native to North America and have spread to many regions of continen-

tal Asia, resulting in serious negative effects on biodiversity and the structure and function of invaded ecosystems (Wan and Wang, 1990; Richter et al., 2013). Pollen from these wind pollinated species and resulting allergies during continental range expansion in favorable regions has made them a great concern, especially under the context of climate change. Understanding and mapping the geographic distribution and change in the potential range of these allergenic ragweed species are important for prioritising prevention and control actions as well as assessing climate impacts of allergy-inducing plant species on human health.

Species distribution models (SDMs) are an important tool for identifying environmental factors affecting a species' distribution and for predicting its potential geographic range. This method has been successfully employed as a useful first approximation to explore climate change impacts on range expansion of *Ambrosia* species in European countries (Cunze et al., 2013), Australia (Dullinger et al., 2009) and Asia (Qin et al., 2014). Of the 46 species in the genus *Ambrosia*, *A. artemisiifolia* is the most widespread species worldwide and by far most

\* Corresponding author. Tel.: +86-20-85280211; fax: +86-20-85281887.  
E-mail address: jeanzh@scau.edu.cn (J. E. Zhang).

studied. Although this species has recently colonized many rural and agricultural habitats in several regions of Asia (Nagada, 1972; Wan and Wang, 1998; Washitani, 2004; Lee et al., 2010; Kim and Kil, 2016), little research attention has been given to its invasive potential. Uncertainties regarding its spatio-temporal spread pattern, potential distribution, and ecoregions that may be susceptible to this species in Asia remain. Several species with high allergenic potential in the same genus, for instance, *A. trifida* and *A. psilostachya* have received attention from European ecologists and corresponding modeling studies have been published (Deák et al., 2013; Rasmussen, 2013), while in Asia, these allergenic plants were insufficiently investigated by far.

As an empirical approach that relates occurrence of a species to environmental predictor variables by formulating statistically or theoretically derived response surfaces, a series of inherent limitations to SDMs have been increasingly reported (Guisan and Thuiller, 2005). Some constraints in using distribution models relate to ecological factors/processes (i.e. dispersal capacity, adaptability) that determine species' distributions and abundances, whereas others are methodological and concern the manner in which data are used in SDMs (i.e. occurrence records, climatic predictor variables, modeling algorithm). There have been substantial efforts and achievements in improving the statistical bases of SDMs (i.e. Zimmermann et al., 2010). For instance, species distribution models and interacting particle systems were integrated into one framework to achieve improved predictions of the spatio-temporal dynamics of invading species. This combined modelling framework has been used to simulate the invasion of *A. artemisiifolia* in Austria successfully (Smolik et al., 2010). Considering the non-equilibrium between the distribution of *A. artemisiifolia* and its ecological requirements during range expansion, accuracy of SDMs was enhanced by taking account of propagule pressure and restricting model calibration to naturalized populations (Dullinger et al., 2009). In Europe, the potential range of *A. artemisiifolia* was estimated with a species distribution model that correlates native North America distributions and environmental variables (Cunze et al., 2013). These studies provided essential contributions in producing various distributional patterns of *A. artemisiifolia* under climate change. Nonetheless, the choice of what is the most appropriate technique to use for modelling distributions (Elith et al., 2006) is not always agreed upon. This is especially the case when interpreting predictions of species distributions across space and time and when assessing the uncertainty of such predictions. Specific knowledge on the selection of climatic predictors, filtering of occurrence data, levels of complexity fit, and variation in the results associated with the modelling technique are needed to produce more realistic and effective management frameworks.

Among the various correlative species distribution models, maximum entropy (Maxent, Version 3.3.3k, Princeton University; Princeton, NJ, USA) is a most widely used machine learning approach based on presence-only data. This method has been successfully employed to estimate probability of distributions from incomplete information or raw environmental data (Phillips et al., 2006), and showing comparable perfor-

mance to that of several traditional techniques that use presence/absence data, including general linear models and general additive models (Elith et al., 2006; Tsoar et al., 2007). However, Maxent was found to be overly sensitive to modeling parameterizations, and its output depends highly on model complexity and how closely data match assumptions (Phillips and Dudík, 2008). Recent efforts addressing these issues, for instance, decreasing sampling bias and complexity tuning, provide very helpful approaches in preventing Maxent from over-fitting (Anderson and Gonzalez, 2011; Bystriakova et al., 2012). Additionally, the use of independent evaluation datasets was also recommended as a way to obtain reliable estimates of model performance (Radosavljevic and Anderson, 2014).

In this study, we generated correlative species distribution models based on native and non-Asian occurrence records for the three allergenic ragweed (*Ambrosia* spp.) species using the Maxent approach. For each species, target-group background and spatial filtering were used to account for sampling bias, and optimal model complexity was identified. Predictive performance of each model was evaluated using independent Asian records, and models showing lower over-fitting and higher performance were selected for assessing their future geographic distribution in Asia. Our goals were (1) to provide more realistic predictions of which areas are most susceptible to invasion by the three allergenic ragweed species, and (2) to assess their further spread in Asia under various climate change scenarios. We focused on reducing over-fitting and improving model performance in predicting independent evaluation data via comprehensive data filtering and species-specific tuning experiments.

## 2. Materials and Methods

### 2.1. Study Species

*Ambrosia artemisiifolia* L. (common ragweed-Asteraceae) is an invasive herbaceous annual native to eastern North America that has spread to parts of Asia (Fumanal et al., 2008; Gaudel et al., 2011) and has become troublesome as an aeroallergen and agricultural weed. This species was introduced in Japan at the beginning of the Meiji Era of 1860 ~ 70s (Okuda and Takeda, 1985) and was widely distributed throughout the Japanese islands by the 1950s (Numata and Kotaki, 1975). Allergies caused by *A. artemisiifolia* pollen are second only to those caused by the conifer tree *Cryptomeria japonica* (L.f.) D. Don (Kazinczi and Novák, 2012) in Japan. *A. artemisiifolia* was first introduced into China in the 1930s and has extended its range from northern to southern China, covering more than 20 provinces during the past three decades (Wan and Wang, 1998). The successful invasion of *A. artemisiifolia* into Asia was suggested to be facilitated by repeated introductions from multiple source populations in the native range creating a diverse gene pool within Chinese populations (Li et al., 2014). The increasing spread of *A. artemisiifolia* in Turkey and India is also a serious human health and environmental issue (Kaplan et al., 2002; Zemmer et al., 2012).

*Ambrosia trifida* L. (giant ragweed), a herbaceous summer annual species characterized by rapid growth and strong competitive ability (Abul-Fatih et al., 1979), is also known as inva-

ders with high allergenic potential in Asia. This species was introduced into Japan in the 1970s or 1980s (Washitani and Nishiyama, 1992) and colonized (semi-) natural habitats. In Japan, this species has been classified as a Rank A species (i.e. one of the 16 most invasive species) because of its substantial deleterious effects on biodiversity and ecosystem function and stability (EFSA Scientific Committee, 2011). The first *A. trifida* populations were observed in northeast China around 1935. The increased occurrence of *A. trifida* has been reported mainly in Beijing, Hebei since the 1950s. The distributional range of this species has now expanded into the central and northern parts of the country (Yin et al., 2010). *A. artemisiifolia* and *A. trifida* are thought to have been introduced to Korea during the Korean War (Park et al., 2002; Lee et al., 2011) and their serious adverse effects on ecosystems were ultimately recognized in South Korea (Republic of Korea) in the 1970s. Both species are now legally designated as “Invasive Alien Plants” in South Korea, where their import, cultivation and use are banned (Kil et al., 2004). Interestingly, *A. artemisiifolia* was reported to have spread into North Korea from South Korea through natural means (Pak and O, 2006).

*Ambrosia psilostachya* DC (perennial ragweed), is an erect, coarse herbaceous perennial with horizontal running rootstocks that is less common in Asia relative to the other two ragweed species. This perennial was introduced into Japan in the 1970s (Nagada, 1972) and is also responsible for increasing the incidence of allergies in the country. *A. psilostachya* has also been reported in Kaohsiung County, Taiwan (Tseng and Peng, 2004) and recently was reported to have established and spread to vast agricultural areas in Karnataka, India (Prasad et al., 2013).

When using SDMs to predict the potential distribution of invasive species, models trained primarily on occurrence datasets from the species' native range need to be transferred to the region where it has been introduced. Models calibrated using combined occurrence records from the native and invaded regions have been recommended for a more complete understanding of species' climatic requirement. While for SDMs trained in the native range, model transferability could be improved by a set of procedures including reducing geographic sampling bias, using fewer environmental dimensions and limiting the model complexity. To examine the strategies that may helpful to improve the predictive power of SDMs for *Ambrosia* species, two SDMs calibrated on two occurrence datasets (native vs. non-Asian range) for each *Ambrosia* species were generated. For each SDMs, species-specific tuning strategies were conducted to obtain the best performing model for the species studied.

## 2.2. Species Occurrence Data

Occurrence records for the three *Ambrosia* species were sourced from the Global Biodiversity Information Facility Data Portal ([www.gbif.org](http://www.gbif.org), 2016) and three databases mainly from Asia: (1) Chinese Virtual Herbarium databases ([www.cvh.org.cn](http://www.cvh.org.cn), 2016), (2) Plants of TAIWAN (<http://tai2.ntu.edu.tw>), (3) Natural History Collection Database, Tokyo (<http://www.kahaku.go.jp>). Occurrence records retrieved from published scientific research literature, museum collections, reports of field

surveys, were integrated and checked. Duplicates (i.e., records of the same specimen sent to different collections; multiple records of a species from a particular location; latitude/longitude equal to 0°) were removed from the datasets. Georeferenced records from the years 1950 to 2000 in this dataset were selected to match with the time-scale of the climate data. Records with unknown date or lack of coordinate data were removed. To minimize spatial bias (i.e. clustering) of occurrence data, one record was randomly selected within each grid cell ( $9.3 \times 9.3$  km). The taxonomic status of all *Ambrosia* species was checked and verified using The Plant List (<http://www.theplantlist.org>) to ensure that the species names and corresponding synonyms were properly assigned. To reduce the effects of sampling bias, a spatial filtering method based on climate heterogeneity using the program SDMtoolbox (Brown, 2014) was employed to select optimal calibration data sets. This spatial filtering method has been suggested to consistently improve model discriminatory ability independent of the initial biases (Procter et al., 2015; Préau et al., 2018), and was expected to account for topographic and climatic heterogeneous across the studied Eurasian continent. With this method, the first three principal components were calculated for all input climatic variables and then used to measure the spatial heterogeneity. The study area was split into areas of high and low climate heterogeneity, for which the occurrence records were filtered at a resolution of 5 and 25 km respectively. The resulting dataset used to build Maxent models contained 644 locations for *A. psilostachya* (native range: 572), 1282 unique occurrences for *A. artemisiifolia* (native range: 556), and 386 locations for *A. trifida* (native range: 347). Contemporary records of the three *Ambrosia* species in Asia not using spatial filtering (513, 468 and 26 for *A. artemisiifolia*, *A. trifida* and *A. psilostachya*), were used as independent datasets to evaluate model accuracy (Table 1).

## 2.3. Background Points

The selection of background values is an important issue when using presence-only modeling. MaxEnt by default uses randomly generated background locations and derives information from those locations for model development (Phillips et al., 2006). Random selection in this case, has been proved to largely affect the predictive performance of the models (Ferrier et al., 2002) and predictions of species distributions (Pokharel et al., 2016). A practical approach may be to select background data from points where similar taxa have been documented (the ‘target group background’ method), so that similar sampling biases are present in the occurrence and background data sets (Phillips et al., 2009). This approach has been found to be more objective and realistic than taking the background sample from sites that have not been sampled and is likely to improve model performance (Marshall et al., 2015). In our study, the target group sample was produced using occurrence datasets for global *Ambrosia* spp. available from the GBIF and supplied databases, which included 6639 unique sampling locations for 46 species of this taxon (1950 ~ 2000). There were 6155 locations for *A. psilostachya* (native range: 3687), 4673 unique locations for *A. artemisiifolia* (native range: 3718) and 6211 locations for *A. trifida* (native range: 4004) and within each 5-arcmin

**Table 1.** Performance Indicators of the Model with Lowest AICc Value for the Three *Allergenic Ambrosia* Species.

Species	Model	$\beta$ -multiplier	Variables	Samples	Background points	Parameters	Loglikelihood
<i>A. psilostachya</i>	Non-Asian model	1	11	644	5142	106	-8320.57
	Native model	2.5	4	572	3687	33	-7600.15
<i>A. artemisiifolia</i>	Non-Asian model	0.5	11	1282	4153	146	-17590
	Native model	1	11	556	3718	70	-7771.32
<i>A. trifida</i>	Non-Asian model	1.5	11	386	5487	35	-4937.11
	Native model	1	5	347	4004	40	-4448.73
Species	AIC	AICc	BIC	AUC. Test	AUC. Train	AUC. Diff	
<i>A. psilostachya</i>	16853.14	16895.38	17326.72	0.8485	0.8836	0.0351	
	15266.29	15270.46	15409.81	0.8090	0.8242	0.0152	
<i>A. artemisiifolia</i>	35472.03	35509.85	36224.84	0.8799	0.9009	0.0210	
	15682.63	15703.17	15984.96	0.8826	0.9083	0.0257	
<i>A. trifida</i>	9944.213	9951.413	10082.67	0.8715	0.8901	0.0186	
	8977.451	8988.17	9131.424	0.8678	0.8964	0.0286	

\* Native and Non-Asian model were Maxent models created based on North America occurrences and global occurrences omitting those in Asia, respectively.

grid cell in the background (Table 1). Based on these aggregated target-group datasets, the background space for each *Ambrosia* species in native North-American and non-Asian ranges was created respectively, from which a set of 10,000 points were randomly sampled for generation of Maxent model.

## 2.4. Current and Future Climate Datasets

The 19 bioclimatic variables reflecting aspects of temperature, precipitation and seasonality, averaged over a 50-year time period (1950 ~ 2000) at 5-arcmin spatial resolution ( $9.3 \times 9.3$  km) were downloaded from the WorldClim dataset (Hijmans et al., 2005). Based on assessments of local botanists and weed management specialists, eleven bioclimatic variables were selected as the most appropriate predictor variables for the envelope models and were projected the WGS84 geographical coordinate system. To avoid multicollinearity among these candidate predictor variables and to reduce model overfitting, the R package “MaxentVariableSelection” (Jueterbock, 2015) was employed for the regularization multiplier ( $\beta$ ) determination, environmental variable selection and model performance assessment by Akaike information criteria, AICc (Akaike, 1974). The variable selection process was performed for  $\beta$  values ranging from 1 ~ 5 in increments of 0.5. Higher  $\beta$  values penalize the inclusion of parameters, thus creating less complex models than the default ( $\beta$  values = 1). Bioclimatic variables with a contribution of less than 5% were eliminated, and all absolute pairwise correlations of the final variables selected for each model were less than 0.75 (Dormann et al., 2013). The best model parameters were selected according to the lowest AICc and were used for current and future distribution predictions of *Ambrosia* species.

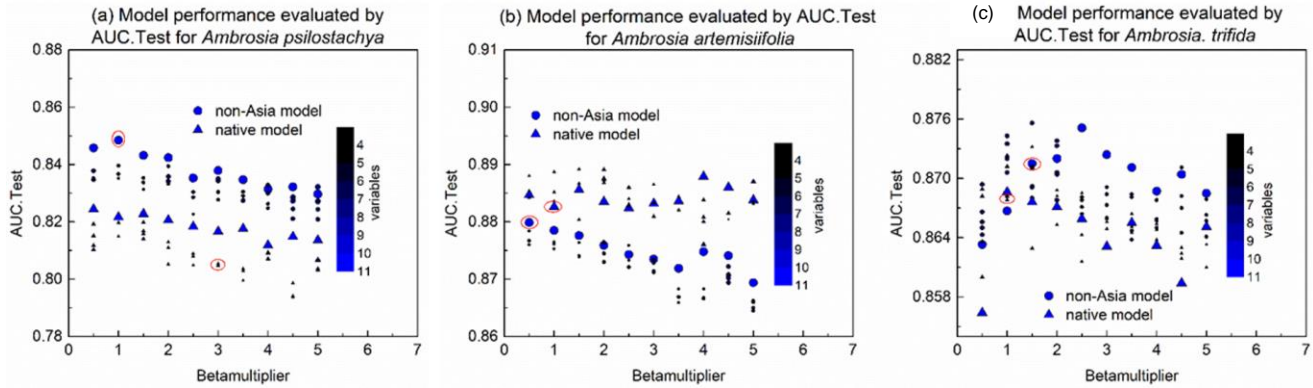
Future climate projections for the year 2050 were derived from four Global Climate Models: CNRM-CM5, HadGEMs-ES, MIROC5, and BCC-CSM1.1. The first three models proved to be among the best models in the global monsoon assessment (Lee and Wang, 2014) and are reliable for future projections in typical monsoon domain region (i.e. Asia). The Beijing Climate Center Climate System Model (BCC-CSM) was used

because this model performed well in simulating the concentration and temporal evolution of atmospheric CO<sub>2</sub> during the 20th century with anthropogenic CO<sub>2</sub> emissions. This last model also contributed to the Coupled Model Inter-comparison Project phase five (CMIP5) in support of the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) (Li, 2014). Two types of representative concentration pathways (RCP4.5 and RCP8.5) were used, in which the RCP4.5 is a stabilization scenario where total radiative forcing is stabilized at about 4.5 W m<sup>-2</sup> after 2100, while RCP8.5 is the high emission scenario where the radiative forcing continues to increase until the end of the 21st century (Rogelj et al., 2012).

## 2.5. Model Development and Evaluation

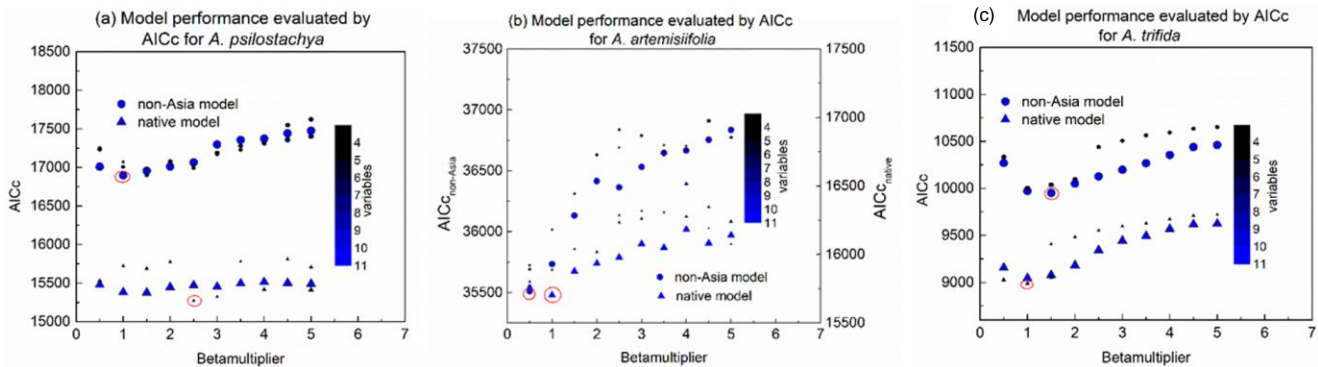
For each allergenic *Ambrosia* species, native and non-Asian calibrating models were created based on North America occurrences and global occurrences omitting those in Asia respectively. The model having highest performance (lowest AICc, Table 1), optimal  $\beta$ -multiplier and sets of climatic variables were used to project habitat suitability of each *Ambrosia* species under current and future conditions. Models were run using Maxent software, with a default convergence threshold of 10-5 and a maximum of 5000 iterations. Feature type for the models was set to linear, quadratic, and hinge features, which has been used to keep the models simple and to avoid over-fitting (Kumar et al., 2014). Quadratic responses are suitable for unimodal curves, as expected for fundamental niches (Austin, 2017), and hinge features could allow simpler and more succinct approximations of the true species response to the environment (Phillips, 2008). The 10-fold cross-validation was implemented to assess model fit. The logistic output format with suitability values ranging from 0 (unsuitable) to 1 (optimal) was used (Phillips and Dudík, 2008). The output of Maxent was imported into ArcGIS version 10.0 (ESRI; Redlands, CA, USA) for spatial representation and calculations.

The area under the receiver operating characteristic (AUC) estimated from the independent Asia range testing dataset (Fielding and Bell, 1997) was used to evaluate model discriminatory



Note: The Maxent model was built with native (solid triangle) and non-Asian (solid circle) occurrence records. Each combination of  $\beta$ -multiplier and set of occurrences was simplified through an iterative process variable selection test. The number of variables in each model is indicated by color and size. Models having the lowest Akaike information criterion (AICc) are marked in red for two occurrence datasets.

**Figure 1.** Model performance evaluated by AUC.Test values (the area under the curve of the receiver operating characteristic estimated from the test data) (Fielding and Bell, 1997) for (a) *Ambrosia psilostachya*, (b) *Ambrosia artemisiifolia*, and (c) *Ambrosia trifida*.



Note: Procedures and symbols for each panel are the same as these in Figure 1.

**Figure 2.** Model performance evaluated by the sample-size-adjusted Akaike information criterion (AICc) (Akaike, 1974) for the three *Ambrosia* species.

power. To further assess model over-fitting, the difference between AUC values from calibration and evaluation data (i.e., AUC.Diff) was calculated. The smaller the difference between the two, the lesser the over-fitting present in the model (Warren and Seifert, 2011). Another way to quantify model over-fitting was by comparing threshold-dependent omission rates with theoretically anticipated levels of omission. Using the method interpreted by Boria et al. (2014), the lowest presence threshold (i.e., minimum training presence threshold of Maxent, Pearson et al., 2010) and the 10th percentile presence threshold (i.e., 10 percentile training omission threshold of Maxent) were calculated and averaged as for AUC. The lowest presence threshold has an expected omission rate of zero for evaluation localities and indicates the least-suitable environmental conditions for which a locality was available in the calibration data set. The 10th percentile presence threshold has an expected omission rate of 0.10 and generally leads to a smaller geographical prediction (Radosavljevic and Anderson, 2014).

To determine whether predicted suitable habitats for each

*Ambrosia* species would expand or contract in the future in relation to current potential habitats in full Asian range, a threshold of 0.5 representing a 50% probability for the presence of conditions considered suitable for the species was used to convert the logistic model outputs to binary grids for each *Ambrosia* species (Elith et al., 2010) firstly. Using the methods provided by Hu et al. (2010), potential future range loss and gain respectively were summed, then related to the predicted current range by pixel and calculated the percentage of predicted range change.

### 3. Results

#### 3.1. Model Performance and Variable Contribution

For all three *Ambrosia* species calibrated on non-Asian occurrences, the average AUC.Test values from 10 replicate runs varied between 0.821 ~ 0.880 (Figure 1). Maximum AUC. Test values for each species were greater than 0.85, suggesting that these models had strong predictive ability and could be used to

**Table 2.** Performance Indicators of the Highest Performance (Lowest AICc) for *Ambrosia. Psilostachya*.

Variables	Non-Asian model		Native model	
	Contributions	Correlation coefficients	Contributions	Correlation coefficients
Model	6	6	22	22
$\beta$ -multiplier	1	1	2.5	2.5
bio1	10.1507	-0.0606	15.8609	0.6598
bio2	8.4103	-0.4810	/	/
bio3	2.8756	/	/	/
bio5	16.672	-0.3866	7.3122	1
bio7	3.4572	/	/	/
bio8	4.9497	/	/	/
bio9	0.9054	/	/	/
bio12	28.0920	1	60.2830	-0.4925
bio14	18.6229	0.7391	16.5438	-0.4481
bio15	2.1408	/	/	/
bio19	3.7234	/	/	/

\* Two subsets of bioclimatic variables (contribution greater than 5%) were selected for native and non-Asian models respectively, based on Maxent model runs and evaluation of correlation coefficients for these predictor sets. The native model of highest performance was a combination of  $\beta$ -multiplier (1) and five bioclimatic variables. The non-Asian model of highest performance was a combination of  $\beta$ -multiplier (2.5) and four bioclimatic variables.

\*\* Variable definitions: bio1: annual mean temperature ( $^{\circ}\text{C} * 10$ ); bio2: mean diurnal range ( $^{\circ}\text{C} * 10$ ); bio3: isothermality ( $* 100$ ); bio5: max temperature of warmest month ( $^{\circ}\text{C} * 10$ ); bio7: temperature annual range ( $^{\circ}\text{C} * 10$ ); bio8: mean temperature of wettest quarter ( $^{\circ}\text{C} * 10$ ); bio9: mean temperature of driest quarter ( $^{\circ}\text{C} * 10$ ); bio12: annual precipitation (mm); bio14: precipitation of driest month (mm); bio15: precipitation seasonality; bio19: precipitation of coldest quarter (mm).

**Table 3.** Performance Indicators of the Highest Performance (Lowest AICc) for *Ambrosia. Artemisiifolia*.

Variables	Non-Asian model		Native model	
	Contributions	Correlation coefficients	Contributions	Correlation coefficients
Model	1	1	5	5
$\beta$ -multiplier	0.5	0.5	1	1
bio1	13.5584	-0.1419	3.2347	/
bio2	4.0562	/	3.4858	/
bio3	12.3695	0.02245	19.9199	-0.2701
bio5	6.5446	-0.3540	9.9143	-0.2837
bio7	4.1478	/	4.0208	/
bio8	0.365	/	0.2904	/
bio9	1.2524	/	1.3799	/
bio12	3.5871	/	4.3166	/
bio14	47.8078	1	45.6258	1
bio15	5.1971	-0.5980	6.2096	-0.5611
bio19	1.1140	/	1.6022	/

\* For native model, a combination of  $\beta$ -multiplier (0.5) and five bioclimatic variables has the highest performance. The non-Asian model of highest performance was a combination of  $\beta$ -multiplier (1) and four bioclimatic variables.

\*\* Definitions for bioclimatic variables are the same as Table 2.

discriminate between presence and absence of habitats. When calibrated on native-range datasets, average AUC.Test values remained high (above 0.80). Maximum AUC.Test values for *A. artemisiifolia* reached 0.889. While these values declined for *A. trifida* and *A. psilostachya*, they can still be used for species suitability predictions (maximum AUC.Test value greater than 0.82).

Variation in AUC.Test values were related to the number of variables and regularization multiplier. For instance, AUC.-Test values in native-range *A. artemisiifolia* model varied from 0.878 to 0.890 (Figure 1 b). The highest AUC Test values were observed in the most complex model set with regularization parameter 0.5 and the full set of 11 climatic variables, while the

lowest AUC values were observed in the simplest model set with regularization parameter 1.5 and 4 climatic variables. Performance of models for each *Ambrosia* species evaluated on the basis of AICc values is provided in Table 1. Models built on native-range datasets encompassed fewer most important climatic predictor variables, and had lower AICc values when compared with those from non-Asian datasets (Table 2 ~ Table 4). For instance, the native-range model of *A. trifida*, with a  $\beta$ -multiplier of 1.0, had the lowest AICc (8988.17, Figure 2c). Out of the five climatic variables (contribution greater than 5%), isothermality (bio3) had the highest contribution (31.45%) to the model in discriminating climatic suitability, followed by mean temperature of driest quarter (bio9), and precipitation of the driest month (bio14). When implemented on non-Asian data-



sets, the model built with regularization parameter 1.5 had the lowest AICc (9951.41, Figure 2c). Isothermality (bio3) was still the most influential variable (with a contribution of 33.50%) among the same five most important set of variables. Annual temperature range (bio7) was introduced as a major climatic factor for model performance (21.51%) (Table 4). Similar patterns in the identification of influential variables using different range datasets were detected for *A. artemisiifolia* and *A. psilostachya*. Interestingly, maximum temperature of warmest month (bio5) and precipitation of driest month (bio14) were observed to be generally the most important range expansion factors for the three *Ambrosia* species (Table 2 ~ Table 4).

All the models had an expected omission rate (minimum training presence threshold) of zero and the 10% calibration omission rate close to 0.1 for evaluation localities, suggesting that no over-fitting occurred when using different calibration datasets (Table 5). Models based on native-range datasets had slightly lower 10% calibration omission rates and AUC.diff, showing comparable performance to the non-Asian models. Native-range models for *A. artemisiifolia* had a significantly higher AUC.eval value (AUC.eval = 0.8532,  $P = 0.008$ , Mann-Whitney U test), while models for *A. psilostachya* and *A. trifida* had lower values for this measure, compared with those of non-Asia models. No statistically significant differences in four evaluation metrics (AUC.diff, AUC.eval, and two omission rates) were found between the two range models, except in the AUC.eval value for *A. artemisiifolia*.

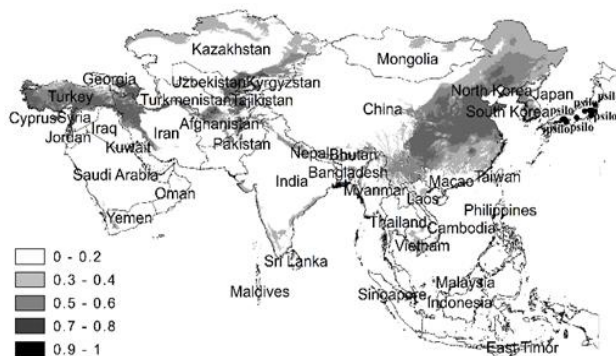
### 3.2. Current Distributions

Distribution maps for each *Ambrosia* species were generated based on native models of lowest AICc in Table 1. Model predictions of the current distribution of these *Ambrosia* species corresponded well with their observed distribution in Asia. Averaged percentage of suitable area for *A. psilostachya*, *A. artemisiifolia*, and *A. trifida* was 10.67, 31.42, and 19.52% respectively (Figure 3). The potential distribution of *A. psilostachya* included parts of the Korean peninsula, north-eastern China, large regions of Turkey and its eastern bordering countries (i.e., Armenia, Azerbaijan, and northwestern Iran). More scattered habitats in northern Mongolia, south-eastern-most Kazakhstan, Kyrgyzstan, Tajikistan, and Afghanistan were also identified as favorable based on the non-Asian model (Figure 3a).

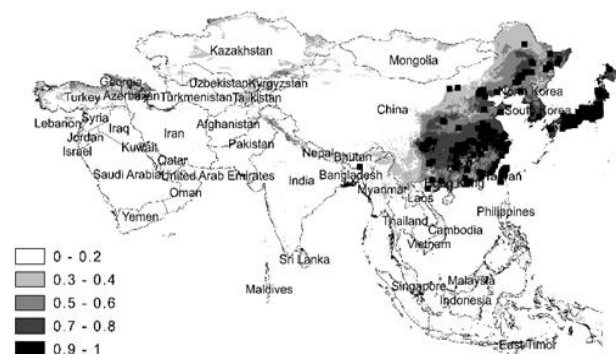
The current estimated range with high occurrence probabilities of *A. artemisiifolia* extended from north-eastern China in the north to the south-eastern coastal areas and as far south as Taiwan. A latitudinally broad potential distribution covering most of the Korean peninsula and Japan as well as Georgia and its southern border areas with Turkey, Armenia and Azerbaijan, eastern Mongolia, were also detected. Small areas of northern Kazakhstan, long zones extending from eastern most Kazakhstan, towards the southeast to northern-most Myanmar, parts of Indonesia, the Philippines and India were identified as being potentially suitable regions, although there are no occurrence records for these regions currently (Figure 3b). The projected distribution of *A. trifida* matched occurrence records in East Asian countries including Japan, the Korean peninsula, and the

north-eastern part of China. Additional suitable areas identified by the model included the border regions of Mongolia, Kazakhstan, and small areas across northern Georgia and Turkey (Figure 3c).

(a) Predicted potential distribution of *A. psilostachya*



(b) Predicted potential distribution of *A. artemisiifolia*

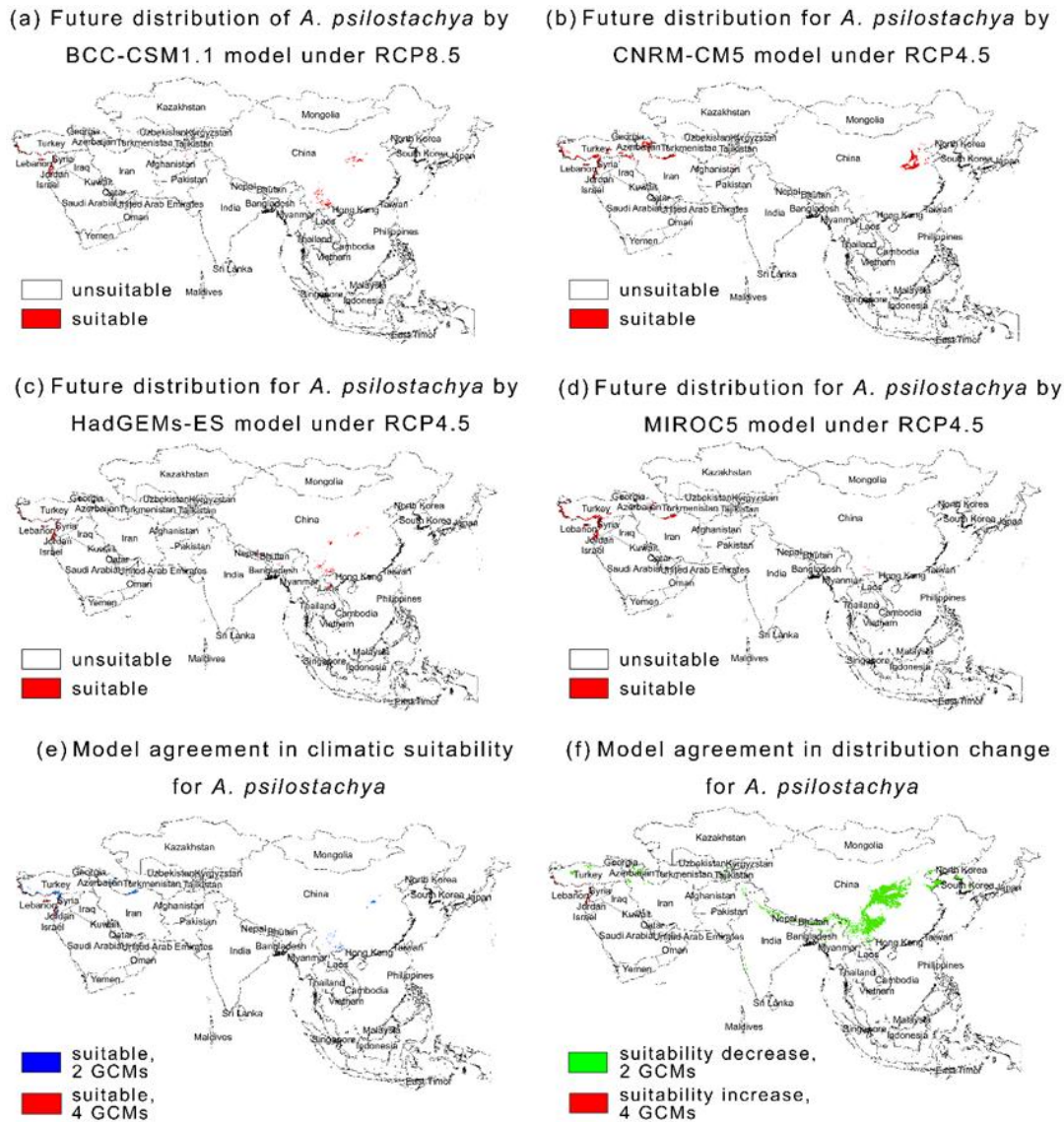


(c) Predicted potential distribution of *A. trifida*



Note: Higher Maxent values in these maps suggest a higher climatic suitability for the species.

**Figure 3.** Predicted potential distribution for (a) *Ambrosia psilostachya*, (b) *Ambrosia artemisiifolia*, and (c) *Ambrosia trifida* in Asia under current climate conditions, with known records shown as dark filled circles, squares and triangles respectively.



**Figure 4.** Projected future distribution for *Ambrosia psilostachya* under the two representative concentration pathways RCP4.5. Maps from left to right (Figure (a) to Figure (d)) show the probability of the spatial distribution in 2050 predicted by four global climate models (BCC-CSM1.1, CNRM-CM5, HadGEMs-ES, and MIROC5). Figure (e) shows modeled agreement in climatic suitability for *A. psilostachya* among the four GCM combinations by 2050, with blue and red color indicating two-GCM agreement and full agreement in suitability respectively. Figure (f) shows projected distribution change in *A. psilostachya* suitability by 2050, showing agreement among a four-GCM ensemble. Areas with current suitability that decreases are indicated in green (four GCMs agreement), whereas areas not suitable in the current time period but suitable in the future are shown in red.

### 3.3. Future Distributions

The selected GCMs and RCPs displayed different variations in area of future suitable climate relative to current conditions for the three *Ambrosia* species (Figures 4 ~ 6). *A. psilostachya* was predicted to spread to areas adjacent to where it is currently present. Future projections of the potential distribution under the two RCP scenarios suggested an overall contraction of *A. artemisiifolia* and *A. trifida* in Asia, despite some areas becoming suitable by 2050.

Almost all of the current suitable areas for *A. psilostachya*

remained favorable and showed a possible expansion under future climate scenarios, with comparable levels of range gain (1.35 ~ 2.49%) and loss (less than 0.05%) across the models and RCP scenarios (Figure 4). Major habitat gains were expected to occur in areas currently suitable for this species, especially parts of Turkey and northwest Iran, Azerbaijan, parts of central and northern China as well as some scattered locations stretching from southern-most Kazakhstan to northern Afghanistan. Under the RCP8.5 scenario, new habitats loss was less when compared to those in RCP4.5, whereas the habitats gain was slightly expand.



**Table 4.** Performance Indicators of the Highest Performance (Lowest AICc) for *Ambrosia. Trifida*

Variables	Non-Asian model		Native model	
	Contributions	Correlation coefficients	Contributions	Correlation coefficients
Model	13	13	9	9
$\beta$ -multiplier	1.5	1.5	1	1
bio1	0.927	/	/	/
bio2	1.4447	/	/	/
bio3	33.4957	1	31.4693	0.0388
bio5	5.7746	0.1170	5.6773	-0.4703
bio7	21.5053	-0.5967	/	/
bio8	0.3242	/	/	/
bio9	18.0684	0.6009	27.4803	-0.2793
bio12	8.5884	0.1386	8.7260	1
bio14	8.7897	-0.2707	26.6471	0.7203
bio15	0.4904	/	/	/
bio19	0.5916	/	/	/

\* The native model of highest performance was a combination of  $\beta$ -multiplier (1.5) and six bioclimatic variables. The non-Asian model of highest performance was a combination of  $\beta$ -multiplier (1) and five bioclimatic variables.

\*\* Definitions for bioclimatic variables are the same as Table 2.

**Table 5.** Performance Evaluation of the Three *Allergenic Ambrosia* Species Using Independent Asian Records

Species	Models	AUCeval	AUCdiff	lowest presence threshold	10% calibration omission threshold
<i>A. psilostachya</i>	Non-Asian	0.7975	0.0687	0	0.0962
	Native	0.7890	0.0221	0	0.0962
<i>A. artemisiifolia</i>	Non-Asian	0.8323	0.0956	0	0.0967
	Native	0.8532	0.0419	0	0.0940
<i>A. trifida</i>	Non-Asian	0.8516	0.0260	0	0.0962
	Native	0.8307	0.0173	0	0.0932

\* Overall performance (AUCeval) and three measures of over-fitting, i.e. AUCdiff (AUCcalib – AUCeval), and average omission rates (lowest presence threshold and 10% calibration omission threshold) on averages of 10-fold cross-validation were provided for the native and non-Asian model, respectively (Boria et al., 2014).

\*\* Note that the native model for *A. artemisiifolia* showed a significantly higher value for the measure of overall performance and a lower value for measurements of over-fitting compared with the non-Asian model.

Based on the four GCM predictive maps overlapped for showing the agreement between the models, estimated climatic suitability for *A. artemisiifolia* increased 0.243% and 0.257% under the RCP4.5 and RCP8.5 scenarios by 2050 (Table 6). These gained areas were mainly located in Hunan, Jiangxi provinces and partially scattered along southeastern coastal regions of China. Meanwhile, all the models predicted 1.122% and 2.178% of suitability loss under the two RCPs, within northern and northeastern China, the central and southern Korean peninsula as well as scattered areas in Japan. Compared with the RCP4.5 (Figure 6), the RCP8.5 scenario resulted in a larger habitat suitability loss when predictions were based on the CNRM-CM5 and MIROC5 models (Figure 7).

All the GCMs predicted apparently contractions of climatic suitability areas in Asia for *A. trifida* in future scenarios (Figures 8 ~ 9). Suitable area (probability of presence greater than 0.5) for this species was predicted to loss by 1.84 ~ 4.80% and 4.77 ~ 5.34% under RCP4.5 and RCP8.5 scenarios respectively, despite a suitability gain of 0.02 ~ 2.28%. Models indicated that most regions colonized by *A. trifida* would become unfavorable in the future and tend to decline with increasing RCP levels. This decline was most notable in most northeast North Korea, scattered habitats across the central region of the

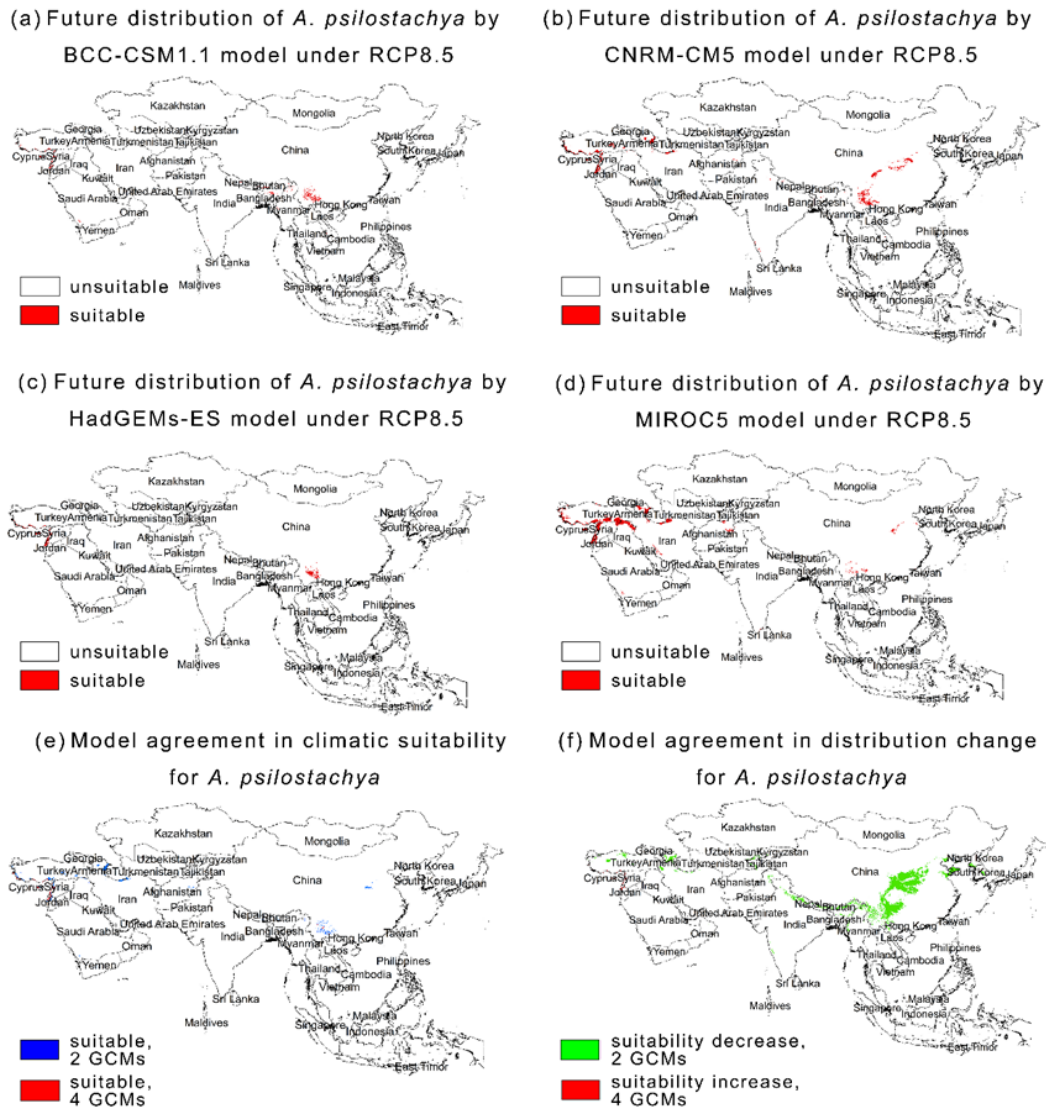
Korean peninsula, eastern China and Japan under RCP4.5 scenario. Under the RCP8.5 scenario, there was less retained and new habitats gain whereas more suitable habitats loss, when compared to those in RCP4.5.

Under both RCP scenarios, predictions using different GCMs under the selected RCPs produced very different outcomes. For *A. artemisiifolia* and *A. trifida*, the highest habitats loss and the consequent narrowest suitable distribution area were predicted by the BCC-CSM and MIROC5 model respectively. For *A. artemisiifolia*, the highest habitat gains and the consequent largest suitable distribution area were estimated by the MIROC5 model. The greatest habitat loss for *A. psilostachya* under the RCP4.5 and RCP8.5 scenarios were obtained from the HadGEMs-ES and MIROC5 models respectively. Notably, *A. artemisiifolia* was predicted to experience a small increase in habitat suitability under RCP4.5 scenario and MIROC5 model, owing to the highest habitat gains.

## 4. Discussion

### 4.1. Potential Distribution and Prospects for Management

The current distribution of *A. artemisiifolia* matched the known occurrence records and indicated that this species had



Note: Maps from left to right (Figure (a) to Figure (f)) present similar information for *A. psilostachya* as illustrated in Figure 4.

**Figure 5.** Projected future distribution for *Ambrosia psilostachya* under the two representative concentration pathways RCP8.5.

considerable potential for successful invasion in Asia. Under future climate conditions, considerable contraction of distribution of *A. artemisiifolia* was expected to occur in most regions having been colonized. Meanwhile, a southwards shift of potential range in China was identified in our study. Contrastly, the potential range of *A. artemisiifolia* in a recent study was predicted to expand and shift northward in Central and Northern Europe by 2080 (Cunze et al., 2013). Plant species are expected to experience spatial (poleward and elevation) shifts in their ranges (Parry et al., 2007) that will influence the abundance and distribution of allergenic plants (Cecchi et al., 2010). The opposite outcome of invasion potential for *A. artemisiifolia* in the two continents provides the evidence of its remarkable adaptive flexibility for range expansion, and raised the concern of whether *A. artemisiifolia* occupy different environmental niche spaces in the two continents. The results also suggested

that recommendations of control measures to prevent *A. artemisiifolia*'s further invasion and the management of potential danger may be different for the two continents.

Projection of *A. artemisiifolia* in Asia showed that, despite the potential range contraction, this species continues to expand its range largely towards adjacent regions located in southern and south-central China, where it has not reached its full distribution potential. Shifts in potential habitats of *A. artemisiifolia* are supported by reports of new occurrences of this species in southeastern China during the last decade, especially in the Zhejiang, Guangdong, Fujian, and Guangxi regions (i.e. Zeng et al., 2010). However, regions in northeastern China including Heilongjiang, Jilin, and Liaoning were found to be barely suitable for colonization both under current and future climate scenarios. This was somewhat surprising given that these are the very regions where the species is generally acknowledged to

**Table 6.** Changes in Climatically Suitable Areas (%) for Three Ambrosia Species by 2050 in Asia Based on Estimations of Maxent Models under the Two Representative Concentration Pathways (RCP4.5 and RCP8.5).

Species		<i>A. psilostachya</i>					
Changes in climatically suitable areas (%) *		Predicted percentage suitable area		Habitat loss		Habitat gain	
RCP4.5	BCC-CSM1.1	1.821		0.02		1.35	
	CNRM-CM5	2.261		0.011		1.78	
	HadGEMs-ES	2.709		0.008		2.225	
	MIROC5	2.468		0.023		1.999	
	Scenario Average **	1.304		0.002		0.863	
RCP8.5	BCC-CSM1.1	2.766		0.043		2.318	
	CNRM-CM5	2.32		0.003		1.831	
	HadGEMs-ES	2.796		0.04		2.345	
	MIROC5	2.976		0.001		2.486	
	Scenario Average **	1.495		0		1.084	
Species		<i>A. artemisiifolia</i>			<i>A. trifida</i>		
Changes in climatically suitable areas (%) *		Predicted percentage suitable area	Habitat loss	Habitat gain	Predicted percentage suitable area	Habitat loss	Habitat gain
RCP4.5	BCC-CSM1.1	1.871	5.966	0.303	4.967	1.84	1.367
	CNRM-CM5	6.527	3.125	2.119	5.209	1.8	1.569
	HadGEMs-ES	5.152	3.711	1.33	5.319	2.397	2.276
	MIROC5	8.708	1.667	2.842	0.934	4.8	0.293
	Scenario Average **	1.561	1.122	0.243	13.605	0.968	0
RCP8.5	BCC-CSM1.1	3.038	5.017	0.522	0.719	4.771	0.05
	CNRM-CM5	5.245	3.431	1.143	0.603	4.859	0.022
	HadGEMs-ES	5.581	3.264	1.312	0.134	5.323	0.016
	MIROC5	6.128	3.212	1.806	0.121	5.335	0.015
	Scenario Average **	2.232	2.178	0.257	6.797	4.287	0

\* Calculation of area based on grid squares identified as  $\geq 50\%$  suitable (Sobek-Swant et al., 2012).

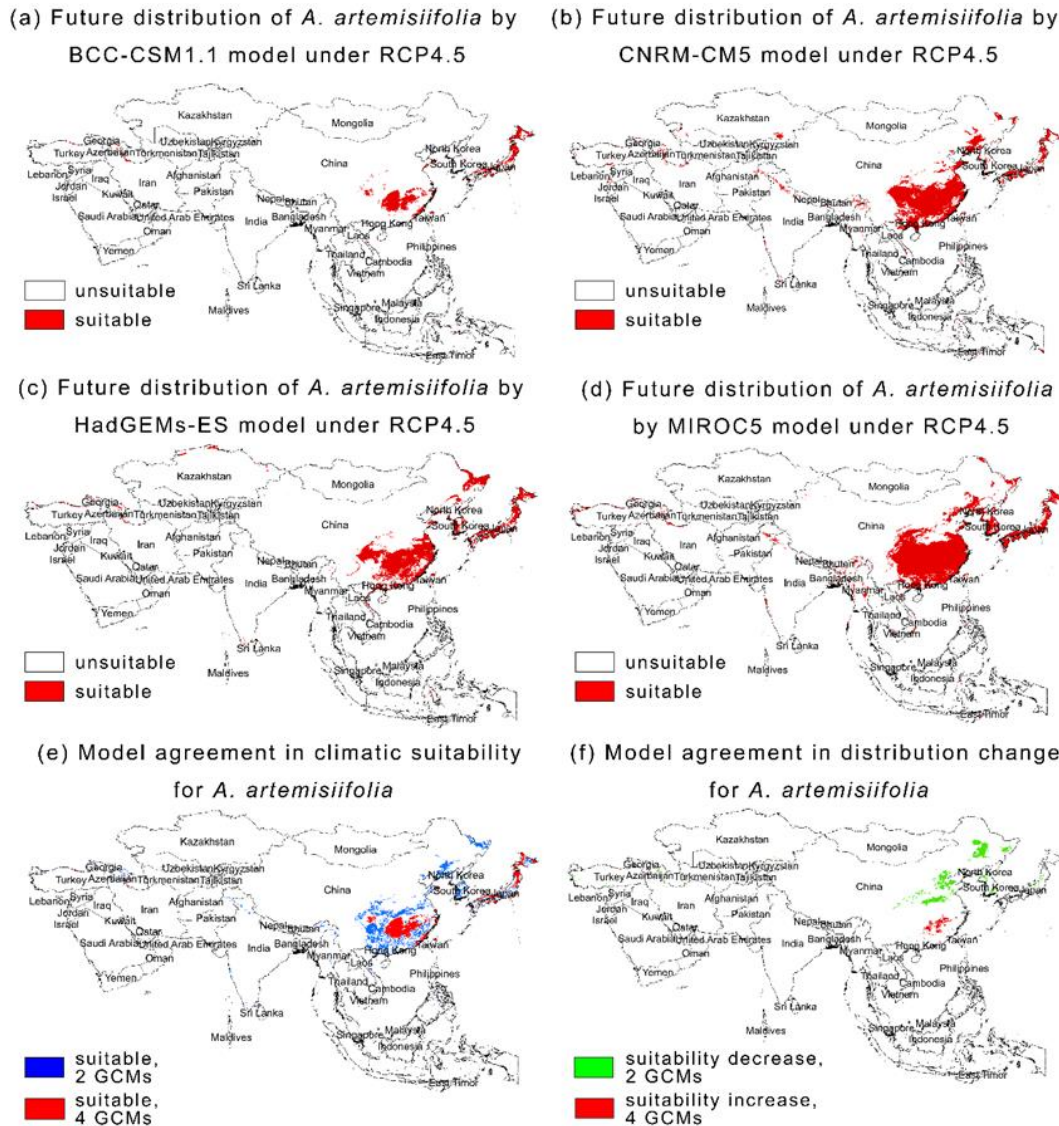
\*\* Calculation of area based on ensemble RCP4.5 and RCP8.5 scenarios using CNRM-CM5, HadGEMs-ES, MIROC5 and BCC-CSM1.1.

have been first successfully introduced (Qi et al., 2011). Whether the pattern in range shift in China contributed to the predicted reduction of climatic suitability for *A. artemisiifolia* in Asia was not assessed in this study.

As an early successional annual plant in the *Asteraceae* family, the presence of *A. artemisiifolia* in a particular region was positively correlated with the length of time since its introduction (Chauvel et al., 2006). The ability of this ruderal species to successfully colonize new areas has been attributed to its potential to produce viable seeds via self-pollination (Bassett and Crompton, 1975). The species is already widespread in western Europe, occurring more commonly in warmer southern regions. In Asia, this species can establish successfully in relatively warmer and wetter conditions owing to its high adaptive ability (Sang et al., 2011). At present, *A. artemisiifolia* may not have occupied all possible suitable regions in Asia, although predictions from our work suggest that it is likely to undergo a range contraction in the future. Nonetheless, over the short-term at least this species is likely to continue to expand its range further south (Figure 5) and as such remains a serious concern from a human health perspective as well as an increasingly problematic weed in cropping systems. Early detection and strategic management plans should thus be put in place for this species, especially in areas with high climatic suitability or recently colonized.

The current climatic suitability for *A. psilostachya* in Asia appears limited, and is primarily confined to Japan. Future projections are for suitable areas to continue to decline for this species due to climate change. The predicted distribution includes several areas (i.e., parts of the Korean peninsula and north-eastern China) that fall outside the ranges having been colonized. These inferred habitats are supported by reports that *A. psilostachya* has established a feral population in Kaohsiung County in southern Taiwan (Tseng and Peng, 2004) and is the second *Ambrosia* species to be found in India (Prasad et al., 2013). The occurrence of *A. psilostachya* far beyond known records suggests that these newly colonized regions may potentially be susceptible to negative ecological impacts and the human population to increased allergy risk from this species. Developing habitat-specific monitoring and control plans to prevent its further spread is important since there is still the potential of a slight gain in suitable habitats under future climate projections.

*A. trifida* remained largely restricted to regions already colonized and showed a potential of substantial range contraction with the radiative forcing level, despite a very limited suitable habitat gain. Results from the four GCMs under RCP8.5 indicate that *A. trifida* might attain its range limit by 2050, highlighting the potential unfavorable effects of climate change for this species. Most of the unsuitable areas were concentrated



Note: Figure (a) to Figure (f) in the two RCP scenarios present similar information for *A. artemisiifolia* as in Figure 4.

**Figure 6.** Projected future distribution for *Ambrosia artemisiifolia* under the two representative concentration pathways RCP4.5.

in northeast China, which is consistent with previous studies (Guo et al., 2004; Qin et al., 2014). In addition to the influence of changing climate on its spread, *A. trifida* has a relatively low fecundity, a transient seedbank and a high percentage of non-viable seeds (Harrison et al., 2007), features which may have constrained its establishment and spread.

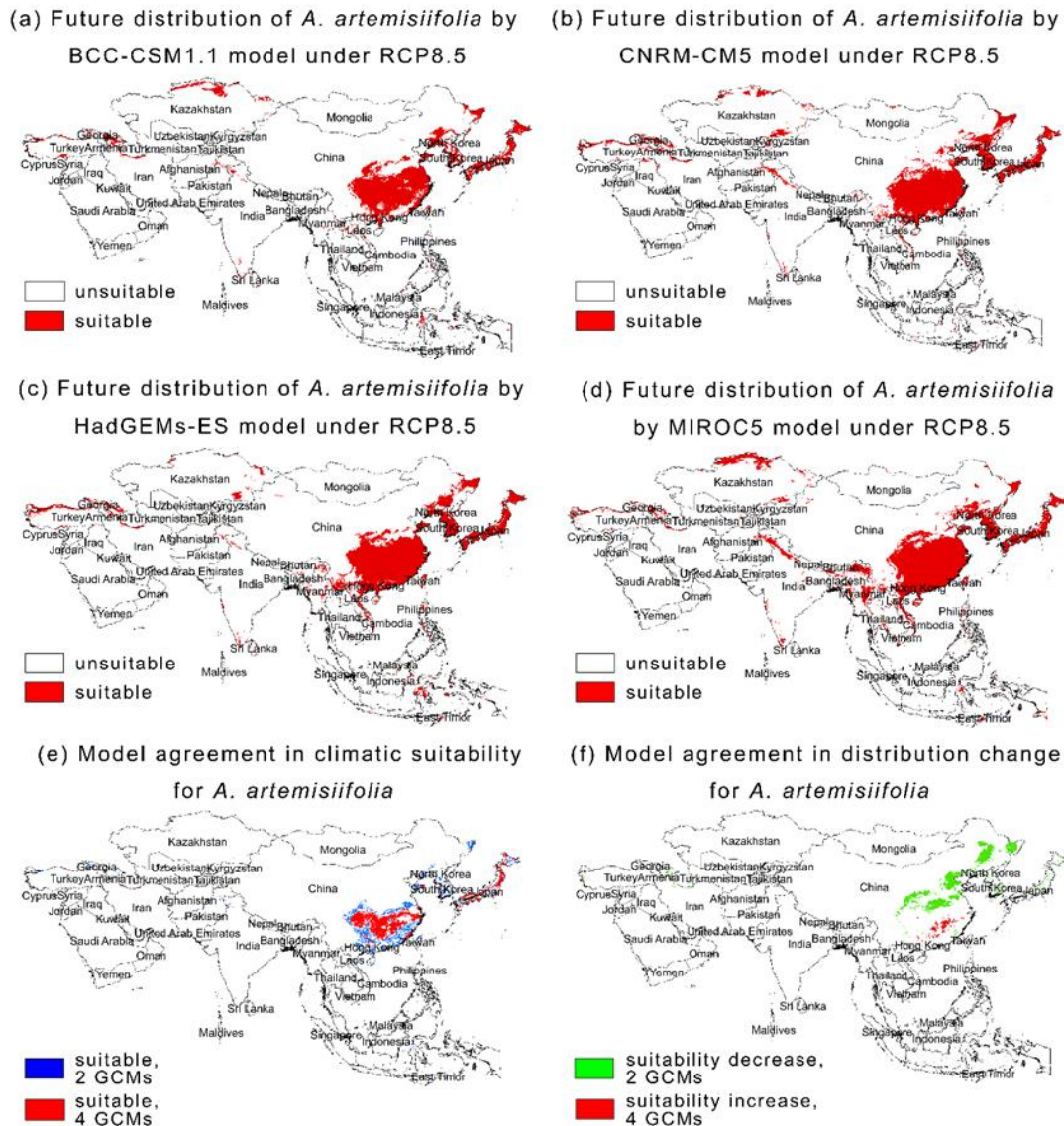
Similar to findings in Europe (Smith et al., 2013), both *A. psilostachya* and *A. trifida* were less abundant in Asia than in other regions. *A. psilostachya* was considered to have less potential for spread and establishment than the other two *Ambrosia* species, as it reproduces mainly by rhizomes and produces few seeds (Gerber et al., 2011). *A. psilostachya* has persisted primarily in Japan since the 1970s but has not spread extensively to neighboring countries (Nagada, 1972; Auld et al., 2003). *A. trifida* was first reported around 1935 in China (Yin et al.,

2010) and was widely distributed throughout the Japanese Islands by the 1950s (Makino, 1985). Despite the high competitive ability and rapid growth rate of this species, few newly established populations have been recorded since the 1970s. During its rather lengthy invasion process, *A. trifida* has spread slowly near previously colonized habitats, and its projected range expansion is likely to be limited especially under more severe climate change scenario. Nonetheless, at present, *A. trifida* still poses a serious threat for eastern Asia because of its high allergenic potential, hence intensive and effective preventive measures are needed in regions where it is expected to establish in the coming years.

#### 4.2. The Effects of Model Complexity

Model complexity (defined as the number of parameters





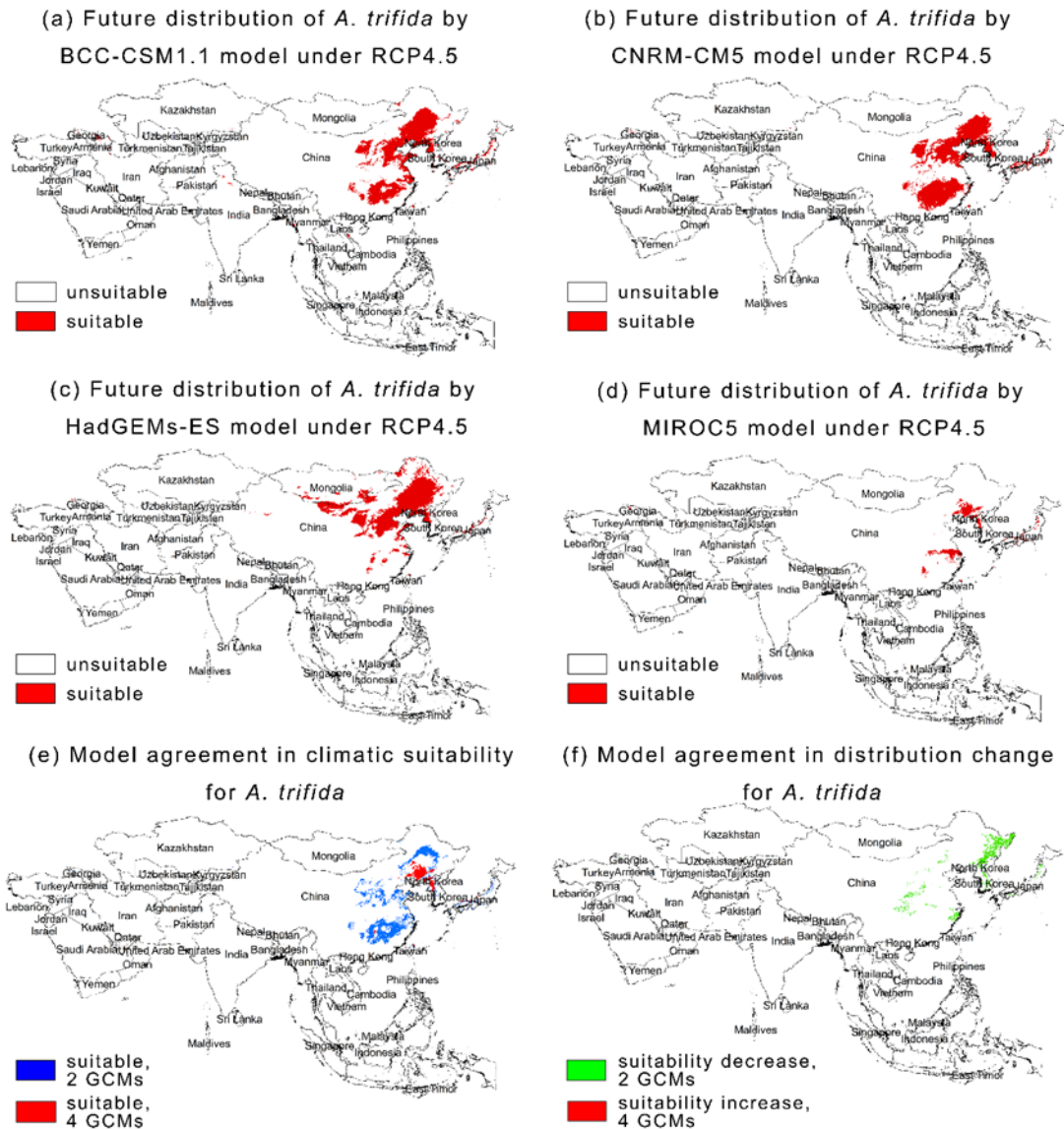
Note: Figure (a) to Figure (f) in the two RCP scenarios present similar information for *A. artemisiifolia* as in Figure 4.

**Figure 7.** Projected future distribution for *Ambrosia artemisiifolia* under the two representative concentration pathways RCP8.5.

included in a model) has been suggested to affect transferability and uncertainty of models in recent studies (Warren et al., 2014; Moreno-Amat et al., 2015). We limited the complexity of *Ambrosia* models in this study through: (1) assessing bioclimatic variables and the correlations among them; (2) changing feature classes and regularization multiplier in Maxent. Results indicated that the effects of model complexity on the predictive performance of models were different for the three *Ambrosia* species. This occurred despite the fact that the best model (in terms of AUC test values) was the one run with all climatic variables (11 variables) and LQH features, but differed in the optimal  $\beta$ -multiplier and calibration datasets. For *A. psilostachya*, higher AUC test values were obtained with the most complex model (106 parameters) using a relatively lower  $\beta$ -multiplier ( $\beta = 1.0$ ) in the non-Asian model. For *A. artemisiifolia*, the

simpler native-model (70 parameters) using  $\beta$ -multiplier ( $\beta = 1.0$ ) resulted in the higher performance. For *A. trifida*, the simpler non-Asian model (35 parameters) using a higher  $\beta$ -multiplier ( $\beta = 1.5$ ) resulted in the higher AUC test values. The effects of model complexity were also reflected in current distribution predictions of the three *Ambrosia* species (Figure 3). The simpler model (based on native or non-Asian datasets) using a relatively higher  $\beta$ -multiplier predicted more potential suitability areas for both *A. Artemisiaifolia* and *A. trifida*, while the higher suitability values were estimated using the more complex non-Asian model for *A. psilostachya*. That higher level of complexity models might not always result in the best model projections is consistent with recent studies in which models of intermediate complexity offered the best trade-off for predicting species distributions across time (Moreno-Amat et al., 2015).





Note: Figure (a) to Figure (f) in the two RCP scenarios present similar information for *A. trifida* as in Figure 4.

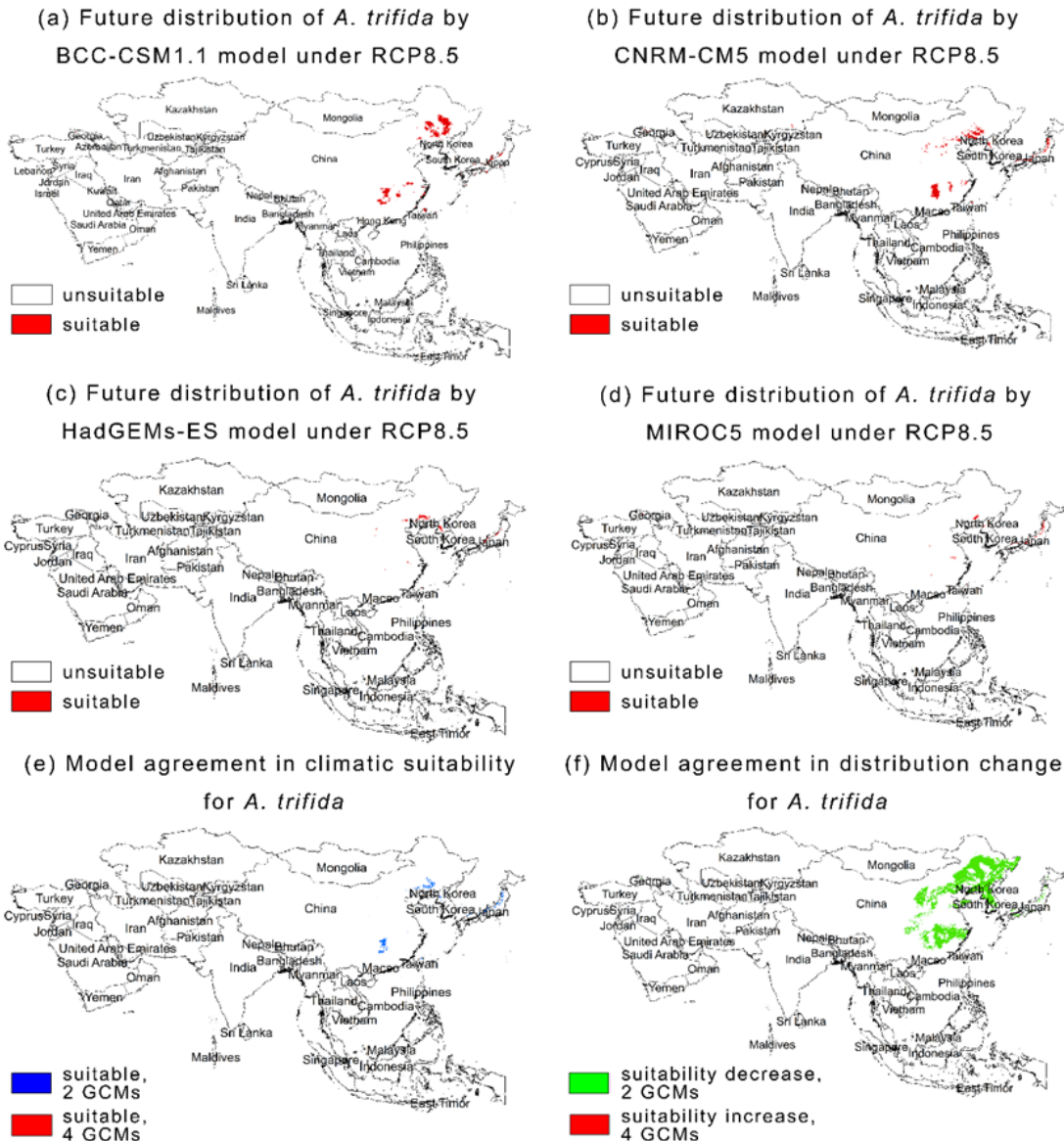
**Figure 8.** Projected future distribution for *Ambrosia trifida* under the two representative concentration pathways RCP4.5.

However, Maxent models based on native-range datasets generated the same level of overall predictive ability and slightly lower overfitting in predicting independent evaluation datasets from Asia. The findings confirmed that reducing the complexity of models is effective in enhancing overall performance and transferability. Thus, performing tuning practice on feature classes, the regularization multiplier, the number of environmental predictors, and sample size, are highly recommended for appropriate model complexity. This is especially important for studies on invasive species using predictive species distribution models for which high spatial transferability are required. On the other hand, although the three *Ambrosia* species showed similar optimal parameters (relevant to model complexity) for best spatial transferability among them, which factors had the greatest effects still remains unclear. Predictive power

of these models that depends on program settings involving sampling bias, parameters of model complexity, geographic background, and size of datasets, should be evaluated using reliable and independent datasets in future studies.

### 4.3. Uncertainties

Previous studies indicated that species distribution modeling techniques generally contributed the largest variation among of the sources of uncertainty in the projection of climate change impacts (Buisson et al., 2010). Ensemble forecasting approaches as well as climate models, thus, were emphasized and widely used to enhance the reliability of projected future species distributions (i.e. Araujo and New, 2007). The interpretation of resulting predictions does not consider the variability caused by



Note: Figure (a) to Figure (f) in the two RCP scenarios present similar information for *A. trifida* as in Figure 4.

**Figure 9.** Projected future distribution for *Ambrosia trifida* under the two representative concentration pathways RCP8.5.

different climate models and/or emissions scenarios (Porfiro et al., 2014), and may be affected by the methods which were used to combine a range of species distribution maps (i.e. Marmion et al., 2009). Using only the Maxent model in our study, high predictive ability was achieved by the fine-tuning of model settings (i.e. occurrence thinning, predicted variables selection, model complexity control, etc.) in future projections. Despite the limitations of this approach having been illustrated, the predictive power of Maxent models was improved by occurrence thinning, model complexity control, and background of dataset choice. Based on three robust evaluation statistical values, the resulting models having greatest AUC values and low over-fitting were selected and then employed to future projections for each *Ambrosia* species. The study supports the ideas

of overcoming the limitations of SDMs (i.e. Maxent model in this study) and using the best-performing models for more effective prediction and in turn, helps to making management decisions for these three troublesome plant species (Anderson and Gonzalez, 2011). To facilitate a framework for risk assessment and feasible management strategies and options, uncertainty sources in sampling datasets, general circulation models, gas emission scenarios and their interactions should be partitioned out and quantified for each *Ambrosia* species. Moreover, species' biological attributes should be considered for projecting the change in a species range, as has been suggested in some studies (Buisson et al., 2010; Clements and Ditommaso, 2011). Divergences in the magnitude of potential range changes of the three *Ambrosia* species also highlight the need for a more in-

sightful analysis of uncertainties and their patterns in future work.

## 5. Conclusion

The three most notorious *Ambrosia* invasive species shifting from their original locations to invade new regions has raised considerable concern in Asian regions. Species distribution models are powerful in providing valuable insights on the geographic ranges of these species, for which the maximum entropy (Maxent) approach was employed for this study. The results strengthen the correct interpretation of SDM outputs by seeking the best fit (i.e., the model with the best transferability and performance) for species occurrence datasets. The information thus provided a valuable perspective for exploring the impacts of parameters of a given method for projecting species distributions. It also provided a better understanding of the challenges/uncertainties at different levels of the modeling process.

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