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Predicting invasions of *Wedelia trilobata* (L.) Hitchc. with Maxent and GARP models

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Abstract *Wedelia trilobata* (L.) Hitchc., an ornamental groundcover plant introduced to areas around the world from Central America, has become invasive in many regions. To increase understanding of its geographic distribution and potential extent of spread, two presence-only niche-based modeling approaches (Maxent and GARP) were employed to create models based on occurrence records from its: (1) native range only and (2) full range (native and invasive). Models were then projected globally to identify areas vulnerable to *W. trilobata* invasion. *W. trilobata* prefers hot and humid environments and can occur in areas with different environmental conditions than experienced in its native range. Based on native and full occurrence points, GARP and Maxent models produced consistent distributional maps of *W. trilobata,* although Maxent model results were more conservative. When used to estimate the global invasive distribution of the species, both modeling approaches projected the species to occur in Africa. The GARP full model succeeded in predicting the known occurrences in Australia, while the other models failed to identify favorable habitats in this region. Given the rapid spread of *W. trilobata* and the serious risk of this species poses to local ecosystems, practical strategies to prevent the establishment and expansion of this species should be sought.

Keywords *Wedelia trilobata* · Maximum entropy (Maxent) · Genetic algorithm (GARP) · Predict · Invasive species

Introduction

A large proportion of the world's introduced ornamental plants have become invasive in areas where they were purposely introduced. The intentional import of species for horticultural, landscape, or agricultural purposes contributes most to the presence of alien floras in many regions. For instance, 52 % of naturalized alien plant species in Europe were introduced for ornamental or horticultural purposes (Lambdon et al. 2008), and 82 % of invasive woody plants in the United States were used by the landscaping sector (Reichard and White 2001). In Germany, 50 % of the alien flora consist of deliberately introduced species, and more than half of these are ornamentals (Kühn and Klotz 2003). The deleterious effects of invasive ornamental plants on economies and biodiversity of natural areas have raised serious concerns in recent years.

Wedelia trilobata (L.) Hitchc. [syn. *Sphagneticola trilobata* (L.) Pruski] (creeping oxeye) is a creeping, mat-forming perennial herb native to Central America that has invaded many areas in the tropics and subtropics after its introduction as an ornamental groundcover (Hossain and Hassan 2005; Thaman 1999). The International Union for

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Conservation of Nature (IUCN) lists *W. trilobata* in its 100 of the world's worst invasive alien species (Lowe et al. 2000), and the Florida Exotic Plant Pest Council classifies it as a category II invader (FLEPPC 2014). *W. trilobata* is reported to dominate agricultural lands, roadsides, abandoned urban lands and other disturbed sites. It also naturalizes and becomes invasive along streams, canals, borders of mangroves and coastal strands (Thaman 1999). It spreads vegetatively, and once established forms a dense ground cover that crowds out or prevents other plants from regenerating including native species (Csurhes and Edwards 1998; Wagner et al. 1990). Knowledge about the potential geographic distribution of this aggressive invader can provide better guidance as to which regions are at risk and mobilize planning to prevent its colonization. Numerous surveys and reports detail areas where *W. trilobata* was introduced and subsequently colonized. These data provide valuable insight into the environmental conditions that favor its establishment and spread in new areas (Batianoff and Franks 1997; Koheil 2000; McConnell and Muniappan 1991). However, more detailed information (e.g. predictive ability of distribution models, the effect of species occurrence dataset on range estimates, etc.) is needed to improve our understanding of the spatial distribution and potential range expansion of *W. trilobata* into novel regions.

Ecological niche modeling techniques establish mathematical functions that link potential predictor variables to available occurrence information of a species. These models have been developed and widely used to predict the likely distribution of introduced species based on climatic and edaphic constraints (Elith et al. 2006; Guisan and Thuiller 2005). Recent work has also focused on assessing the underlying assumptions, inherent simplifications, critical limitations and the reliability of these modeling techniques (Rodda et al. 2011; Sinclair et al. 2010; Terrible and Diniz-Filho 2010). Maximum entropy (Maxent; Phillips et al. 2006) and genetic algorithm for rule set production (GARP; Stockwell and Noble 1992), two of the most commonly used presence data-only niche-based modeling methods, have been used for predicting spatial distributions of various species at different scales (e.g. Larson et al. 2010). The two algorithms differ in their rationales and procedures, leading to arguable results regarding their recent performance. For instance, Maxent was more successful than GARP in extrapolating results to new regions (Heikkinen et al. 2012), and showed better predictive accuracy than GARP and other methods (Elith et al. 2006; Hernandez et al. 2006). Townsend Peterson et al. (2007) demonstrated that GARP was more successful in predicting species distributions in broad, unsampled regions than Maxent, as evidenced by the percentage of area a target species was predicted to be present in. When predicting invasion ranges, one important concern is the information (native, invaded or full ranges) used for developing the niche-based models. Models based on data from the native range assume the same environmental factors determine the distribution of the species in the invaded range. However, this assumption may not adequately reflect the distribution of an invasive species in a novel region (Estrada-Peña et al. 2007). Combining native and introduced distribution records in models may be most insightful (Welk 2004), but may not consistently improve model projections (Thompson et al. 2011). Nonetheless, the extent to which the occurrence records represent the environmental space occupied by a target species should be considered when generating these models.

As one of the most commonly introduced ornamental plants, *W. trilobata* has spread across vast regions of the world. It is becoming widely naturalized in South Africa, the southeastern USA (e.g. Florida and Louisiana), tropical Asia (e.g. Indonesia, Papua New Guinea, and southern China), northern and eastern Australia and many Pacific islands (e.g. American Samoa, the Cook Islands, and Fiji), where climate characteristics may differ from those encountered in the native range. Hence, this species is an ideal candidate for investigating variability in predictions using different models and range occurrence data sets. We developed models for *W. trilobata* using the Maxent and GARP modeling techniques based on native and full range (including native and invaded ranges) occurrence records. The objectives of the research were to (1) test the predictive capability of the two modeling methods, (2) determine the most effective method for anticipating the species' global potential distribution, and (3) assess the contribution of the various environmental profiles to model prediction.

Materials and methods

Species occurrence data

Presence records of *W. trilobata* were obtained from the following online herbaria databases: the global biodiversity information facility (GBIF; http://www.gbif.org), Tropicos (http://www.tropicos.org/), Pacific Island ecosystems at risk (PIER) and the University of South Florida Herbarium (http://www.plantatlas.usf.edu/isb/herbarium.htm), as well as Chinese Virtual Herbarium databases, China Species Information System and National Standard Integration of Species Information for teaching and resources sharing platform. Results from other published scientific research literature and reports of field surveys were also included. Records collected during 1950–2000 were used for model building. The dataset was checked in the DIVA-GIS software (Hijmans et al. 2002) and records with obvious geocoding errors were discarded. Duplicate records were removed manually. The resulting dataset was then overlaid with a

10 km grid and one record was randomly selected from each cell, thereby 861 documented global presence records were obtained for constructing the models. Of these, 528 records were collected from the native ranges of *W. trilobata*, i.e. Mexico, Central America (Costa Rica, Panama, Nicaragua, Honduras, Belize, and Guatemala), Caribbean and northern South America (Guyana, Venezuela, Brazil, Bolivia, Colombia, Ecuador and Peru). The remaining 333 records were collected from invaded ranges (North America, Australia and New Zealand, Western Europe, Eastern and Southeast Asia), including 190 occurrence points from China. *W. trilobata* was reported present in West Africa (Liogier and Martorell 2000), however, documented records and museum specimens from the area are very limited and therefore no occurrence record from West Africa was used in the study.

Selection of environmental variables

Climate information derived from the WorldClim 1.4 database at a spatial resolution of 5 arc-min was used to develop the species distribution model (Hijmans et al. 2005). The input data were selected from a total of 48 climate variables that describe monthly total precipitation and mean, minimum and maximum monthly temperature, along with 19 other bioclimatic variables collected from 1950 to 2000. To reduce high collinearity and minimize model overfitting, pairwise correlation analyses were performed first. Variables showing a correlation higher than 0.90 were considered redundant, whilst low-correlation variables were employed to construct the niche models. The subsets of temperature and precipitation redundant variables were then used to perform a principal component analysis (PCA) separately. For each of the PCA factors, variables with the highest (>0.9) factor loadings, measurements for the correlations between the original variables and the factor axes, were selected. This resulted in a final environmental dataset containing 31 temperature and 12 precipitation variables. Grid layers of these variables were clipped with ArcGIS 10.0 (ESRI, Redlands, California, USA) in the assumed native range and the entire invaded range, including China, to make projections in these regions.

Environmental space comparison

Principal component analysis on selected environmental variables was performed to compare the position of occurrences from the native ranges and invaded range in China in multi-dimensional space, following Broennimann et al. (2007). The convex hulls encompassing 95 % of occurrence clouds in the two ranges were identified visually in the PCA bi-plots. Significance differences between the two ranges were further assessed by a between-class analysis and 99 Monte Carlo randomization tests (Romesburg

1985). Differences in the mean values of environmental variables from the native ranges and invaded range in China were tested on individual variables, using Welch's *t* test and Levene's test for homogeneity of variance.

Model development

Maxent and GARP methods were applied to define *W. trilobata* climatic exigencies as a function of related environmental variables. The modeling process consisted of three steps: (1) predictive models were built separately based on point occurrence data from: (a) native range only and (b) full range (native and invasive) using Maxent and GARP approaches; (2) all models were projected into the assumed native range and China for evaluation of invasion distributions. Environmental variations between the native ranges and invaded range in China were investigated; and (3) models were then projected at a global scale to identify areas putatively susceptible to *W. trilobata* invasion.

Maxent

Maxent is a machine learning algorithm based on the maximum entropy principle. It assesses the probability distribution of a species by estimating the probability distribution of maximum entropy (Phillips and Dudík 2008). In this study, Maxent software version 3.3.3 k (Princeton University; Princeton, NJ, USA) was used to predict the probability of *W. trilobata* occurrence and to map its potential spatial distribution. Models were trained using a randomly selected 75 % of occurrence records and then tested on the remaining 25 %. For each training partition, 10 replicates were produced and results averaged. Models were run with default features for the convergence threshold (10^{-5}) and a maximum of 500 iterations. Background points were randomly selected within the area enclosed by a minimum-sized convex polygon that contains all native range or invaded range records. Hinge feature types were used to make simpler and more succinct approximations of the true species response to the environment (Phillips 2008), and a jackknife procedure was used to limit the number of environmental layers to only those layers that affected the distribution of the species. A fade by clamping function was used to remove predicted areas where clamping occurred. The outputs were generated in the form of continuous cumulative probabilities ranging from 0 to 100, with higher values indicating higher probabilities of the areas being suitable habitats for *W. trilobata* (Elith et al. 2006).

GARP

The GARP model predicts environmental niches of species by identifying non-random relationships between

environmental characteristics of known presence localities compared with the entire study region (Mau-Crimmins et al. 2006). In our study, the Desktop GARP application version 1.16 was used as a second approach for predicting the distribution of *W. trilobata*. The same subsets to build and validate Maxent models were used in the GARP model for comparing the two methods. For each model run, the best-subsets selection procedure (Anderson et al. 2003) was used with a convergence limit of 0.01, maximum number of iterations of 1,000, and 20 runs per model. Based on omission and commission errors (Anderson et al. 2003), the best 10 models were identified and summed to create a final output grid of model agreement, ranging from 0 (areas where none of the 10 models predicted the presence of *W. trilobata*) to 10 (areas where all of the models predicted the presence of *W. trilobata*). The rule sets from these 10 models were projected onto the environmental layers for the specified area to generate predictions of *W. trilobata* distribution.

Model evaluation

A re-sampling function in DIVA-GIS was applied to generate five randomly generated sub-datasets by bootstrapping from the original occurrence record dataset. Each sub-dataset comprised 75 % of the species records as training data. Additionally, pseudo-absence points were randomly generated with an equal number of occurrence records for each study range in each sub-dataset. This approach enabled statistical evaluation of replicate model running in DIVA-GIS to objectively compare the modeling performance of distinct algorithms (Giovanelli et al. 2010). The minimum presence threshold was selected to generate a binary map depicting the predicted area for each model. This threshold equals the minimum model prediction area whilst maintains zero omission error in the training data set (Pearson et al. 2007), and has been used for presence-only models, especially for Maxent and GARP methods producing different outputs with very different frequency distributions (De Meyer et al. 2010).

Null models were created and used to test the significance of both Maxent and GARP models (Raes and ter Steege 2007). For each prediction model of *W. trilobata*, 99 null-distributions of random points in the study area were generated. The number of random points per distribution was equal to the actual number of presence points. Models were run in Maxent by relating the null-distributions to the environmental layers for calculation of the average AUC. The AUC value of each randomly generated model was then compared with the AUC of the models generated using the actual distribution data in a one-tailed test ($\alpha = 0.05$). If the AUC of *W. trilobata* models was significantly higher than the AUC of randomly generated models,

the species distribution model performs significantly better than expected by chance (Raes and ter Steege 2007). Model performances were evaluated using an adaptation of the ROC curve approach by plotting omission on an inverse scale (sensitivity) along the y-axis versus proportion of area predicted present (an estimator of 1-specificity) on the x-axis (Peterson et al. 2008; Phillips et al. 2006).

Results

Importance of environmental variables

There were 12 and 15 variables with contributions greater than 1 % identified to be important in creating native and full model fit for *W. trilobata*, respectively (Table 1). Of these environmental variables, average monthly precipitation in September (prec9) and June (prec6) contributed most for the native model (30.82 %) and full model (33.33 %), respectively. Elevation (alt), average monthly precipitation in October (prec10), prec6, average maximum temperature in November (tmax11) and average minimum temperature in April (tmin4) were important variables for both models. When observing the individual importance of each variable to the model, the variables that contributed the most alone (i.e. running the model with that variable only) were prec9, prec10 and average maximum temperature in June (tmin6) for the native model. Annual precipitation (bio12), precipitation of wettest quarter (bio16) and prec6 were the three variables that contribute most alone to the full model. All these variables had generally limited redundant information (model gain varied considerably when the variable was excluded, see Table 1) and therefore their contributions failed to show large differences when projected at a global scale. For the native model, average monthly maximum temperature in December (tmin12) and average precipitation in January (prec1) had the least redundant information and were the variables that impacted model performance the most if excluded. Similarly, precipitation seasonality (bio15) was the most influential variable to the full model.

## Environmental conditions across native and invasive ranges

Principal components analysis (PCA) on environmental layers for the occurrences of *W. trilobata* performed successfully in niche comparisons of environmental space. The first two axes of the PCA were primarily associated with temperature and moisture and accounted for about 62.6 % of the total variation in environmental niches (Fig. 1). The niche centroids of native and invasive populations differed (i.e. between class inertia ratio of 23 %, $P < 0.01$). Five

Table 1 Results of jackknife procedure evaluating the importance of environmental variables (relative contribution >1.0 %) for native and full models

Native model				Full model			
Environmental variables	Percent contribution (%)	With only	Without	Environmental variables	Percent contribution (%)	With only	Without
prec9	30.824	0.984	1.959	prec6	33.331	1.443	2.362
alt	12.979	0.447	1.948	bio16	20.942	1.334	2.378
prec6	12.909	0.678	1.953	bio18	9.058	1.329	2.367
tmean11	9.621	0.420	1.962	prec12	4.793	0.521	2.375
tmax11	7.537	0.616	1.946	alt	4.357	0.491	2.355
tmin6	5.508	0.707	1.964	bio6	2.802	0.951	2.381
prec10	3.249	0.721	1.953	tmax11	2.280	1.002	2.373
tmean12	2.742	0.394	1.960	bio11	2.273	0.842	2.381
prec1	2.176	0.220	1.964	bio15	2.260	0.212	2.380
prec11	1.750	0.342	1.958	bio12	2.160	1.343	2.380
tmin4	1.684	0.341	1.962	prec4	1.916	0.661	2.352
tmin12	1.466	0.207	1.961	tmin7	1.776	1.004	2.382
				tmin4	1.429	0.959	2.377
				tmin11	1.217	0.879	2.381
				prec10	1.160	0.894	2.375

Only variables that contributed >5 % to the native or full models were used for range prediction

Variable definition: *bio6* min temperature of coldest month, *bio11* mean temperature of coldest quarter, *bio12* annual precipitation, *bio15* precipitation seasonality, *bio16* precipitation of wettest quarter, *bio18* precipitation of warmest quarter. *prec4*, *prec6*, *prec10* and *prec12* represent precipitation of April, June, October and December, respectively. *alt* altitude, *tmax11* maximum temperature in November. *tmin4*, *tmin7* and *tmin11* represent minimum temperature of April, July and November, respectively
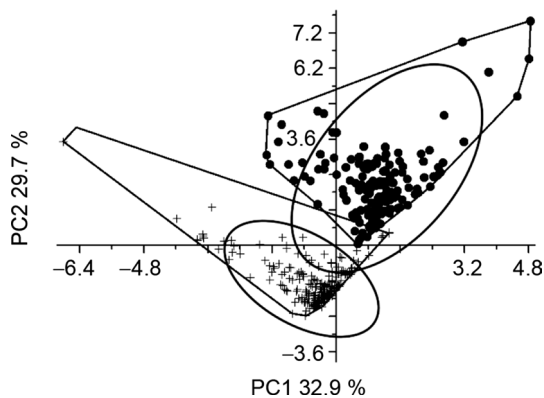
Fig. 1 Principal component analysis (PCA) for environmental variables associated with occurrence datasets of *W. trilobata* in the native range (*red cross*) and China (*black filled circle*). The *ellipses* and *convex hulls* indicate the prevalence (95 and 100 % of sites included) of environments in the study ranges, respectively

thermal and nine moisture variables highly correlated with the first two components were compared in the native range and invaded range in China. Introduced populations of *W. trilobata* could establish in invaded areas with more variable and lower winter monthly temperatures (e.g. tmean1, tmean2, tmean12), minimum temperature of the coldest month (bio6), and mean temperature of the driest (bio9) and coldest quarter (bio11) than native populations (Fig. 2). In China, this species also occurred in habitats where annual precipitation (bio12), precipitation in the wettest (bio16), average monthly precipitation in October (prec10) and November (prec11) were significantly lower and less variable than for the native ranges, despite the greater precipitation in the warmest quarters (bio18).

W. trilobata distribution in the native range

Predictions from the GARP and Maxent models based on separate random testing occurrences were significantly ($P < 0.05$) better than random expectations. The prediction of environmental suitability between native regions and invaded regions in China varied widely across the models (Table 2; Fig. 3). The GARP full model best predicted known distributions in native regions. The model indicated that most regions of Central America, including Guatemala, Belize, Nicaragua, Honduras, Costa Rica, Panama, and the southwestern and southeastern border areas of Mexico were suitable for *W. trilobata* and encompassed 74.58 % of its natural range. High environmental suitability was detected for over half of Central and South America. GARP full model results also suggest that *W. trilobata* may spread

Fig. 2 The most important thermal variables (**a**–**i**) and moisture variables (**j**–**n**) for *W. trilobata* across localities sampled from the native range and China. In *box plots*, the minimum and maximum values are indicated as *short horizontal bars*; the 1st and 3rd quartiles are indicated as *filled circles* and *asterisks* respectively; the median and means are shown as a *broad horizontal bar* and *unfilled square*, respectively. Mean values in the native range were statistically higher than those in China ($P < 0.05$)
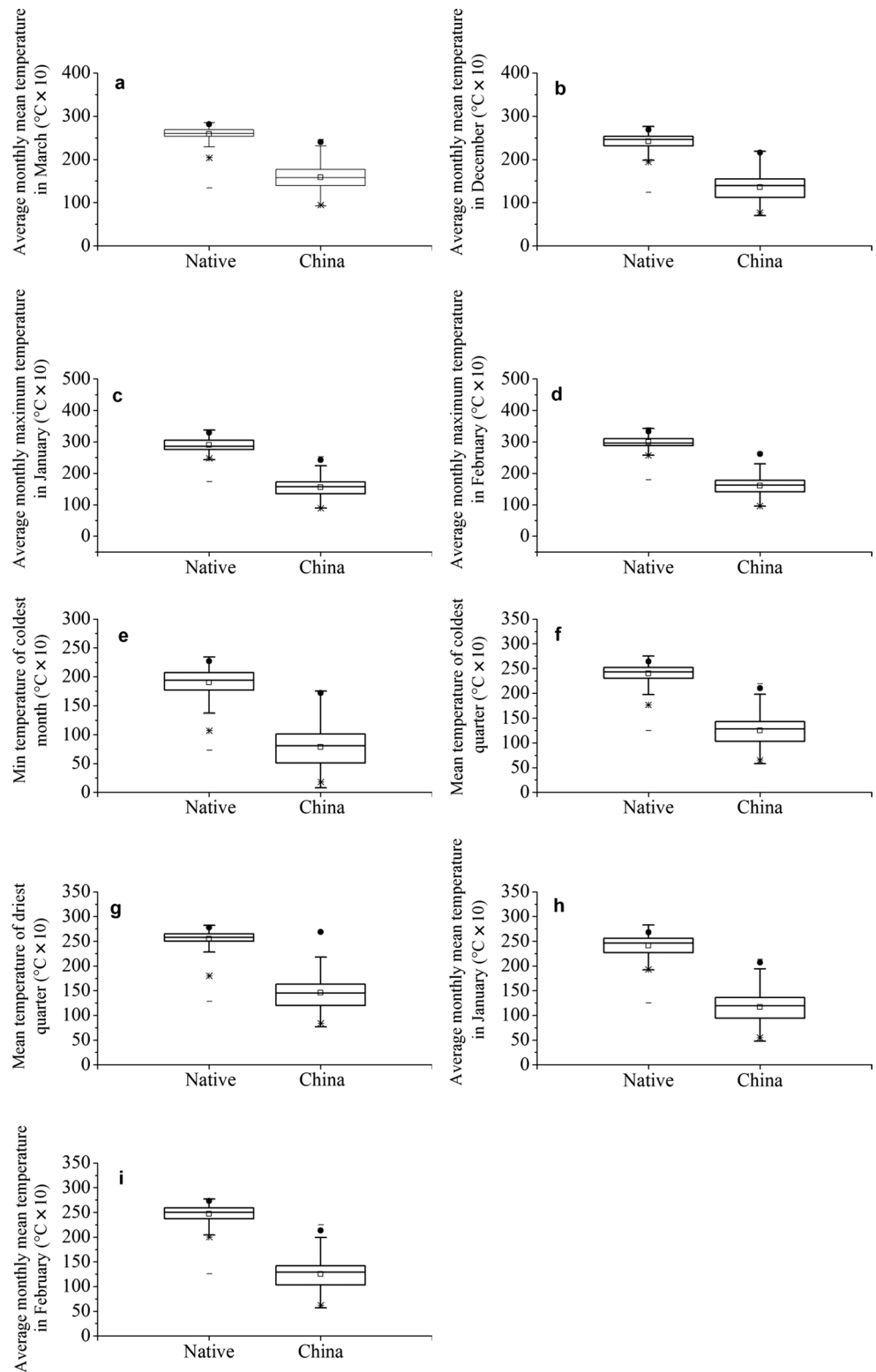
further into interior areas of several countries including Brazil, Bolivia, and Venezuela from border regions where the species is present. The GARP native model predicted an extensive convergent range of spread in Brazil and Mexico. Predicted suitable habitats were restricted in Central American regions and sizable contiguous areas of Venezuela, Columbia, and Ecuador bordering northwestern Brazil (Fig. 3).

Fig. 2 continued
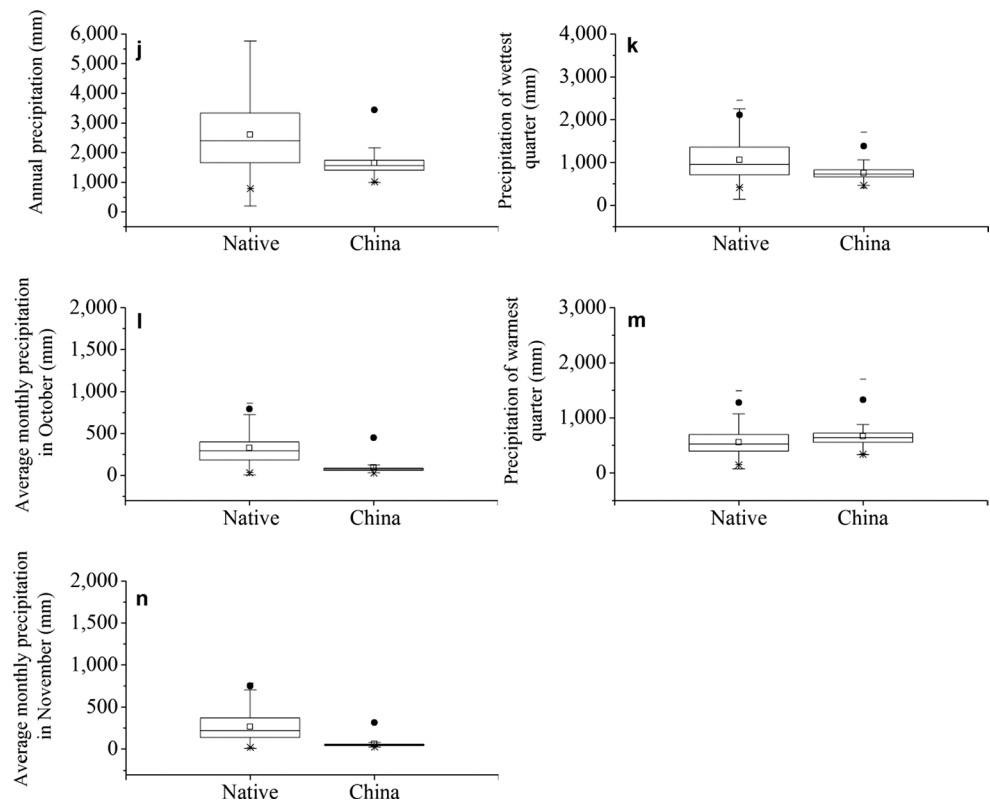
Table 2 Mean AUC values (±standard error, $n = 10$) and prediction results for potential distribution of *W. trilobata* using GARP and Maxent models fitted with: (1) native range data only (GARP or Maxent native model) and (2) all available global data (GARP or Maxent full model)

Model strategies	Native range				China			
	AUC	Percentage of above-threshold areas (%)[c]	Percentage of suitable areas (%)	Percentage of common occupied areas (%)	AUC	Percentage of above-threshold areas (%)[c]	Percentage of suitable areas (%)	Percentage of common occupied areas (%)
GARP full model[a]	0.90 ± 0.017	82.65	74.58	66.46	0.92 ± 0.012	11.90	7.32	9.49
GARP native model[a]	0.83 ± 0.021	67.53	22.13		0.85 ± 0.025	45.32	2.48	
Maxent full model[b]	0.75 ± 0.043	52.30	0.02	49.52	0.83 ± 0.031	14.28	1.05	14.17
Maxent native model[b]	0.78 ± 0.035	76.35	1.28		0.84 ± 0.028	32.71	0.05	

Model predictions were projected in native and invaded China ranges respectively

[a] Calculation of area based on grid squares identified as ≥50 % suitable

[b] Calculation of area based on at least 50 % of the models identifying a grid square as suitable

[c] Areas were calculated after a minimum presence threshold was applied

The Maxent model predictions differed substantially from the GARP model predictions (Fig. 3). Compared with GARP models, the Maxent native models predicted a narrower distribution of *W. trilobata* that may extend from the southern border areas of Mexico to Central America, and connecting with northwestern regions of South America. This species may also be less likely to invade large areas of interior Brazil. The Maxent native model also suggested that suitable environmental conditions may occur in some small areas located in southeastern Mexico, northeastern borders of Belize, Honduras, Costa Rica and Panama. Suitable habitats may also span into western border areas of Columbia. The Maxent full model identified only 0.02 % of the natural range of *W. trilobata* as suitable habitat, largely in the western border regions of Columbia (Table 2; Fig. 3).

W. trilobata distribution in China

The GARP full model performed well in predicting high environmental suitability in most parts of coastal southern
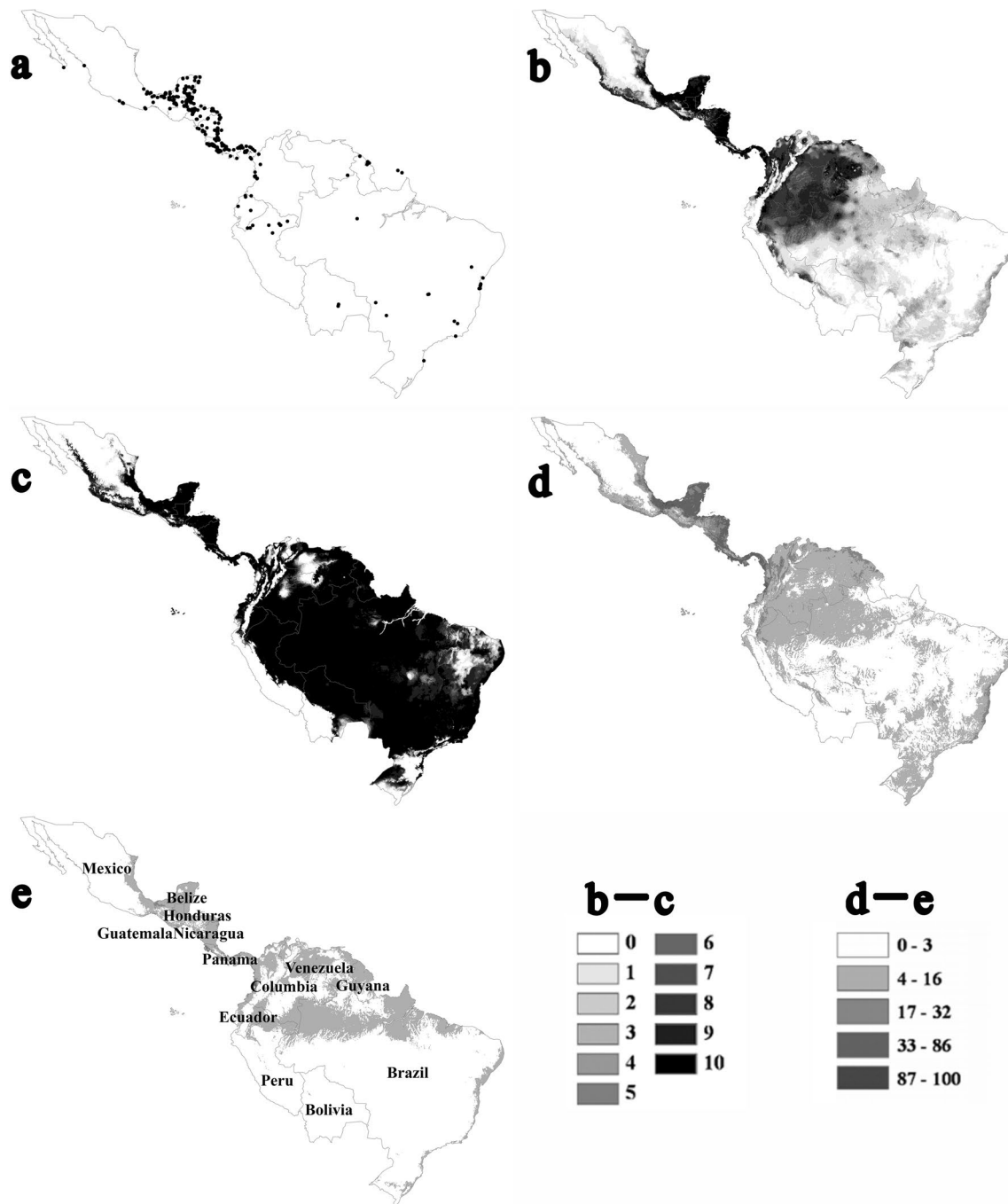
Fig. 3 Occurrence records of *W. trilobata* collected in **a** native range; **f** China; **k** global range. Predicted geographic distribution of *W. trilobata* using GARP models in native range (**b**, **c**), China (**g**, **h**) and global range (**l**, **m**) based on native and full range occurrences respec-

tively were provided, results using Maxent models in native range (**d**, **e**), China (**i**, **j**) and global range (**n**, **o**) based on native and full range occurrences were also included

China, including Hong Kong and the tip of Taiwan (Fig. 3). Regions of southeastern Zhejiang, Jiangxi, Hunan, southern Guizhou, Yunnan bordering on Fujian, Guangdong and Guangxi were also predicted to be environmentally suitable for *W. trilobata*. Although not currently colonized, the contiguous areas between southern Chongqin and southeastern

Sichuan were potentially suitable for establishment of this invasive species. Compared with the full model, the GARP native model predicted the occurrence of *W. trilobata* in more regions along the coast of southeast China and detected suitable areas from these regions. However, the model failed to identify suitable regions extending to the
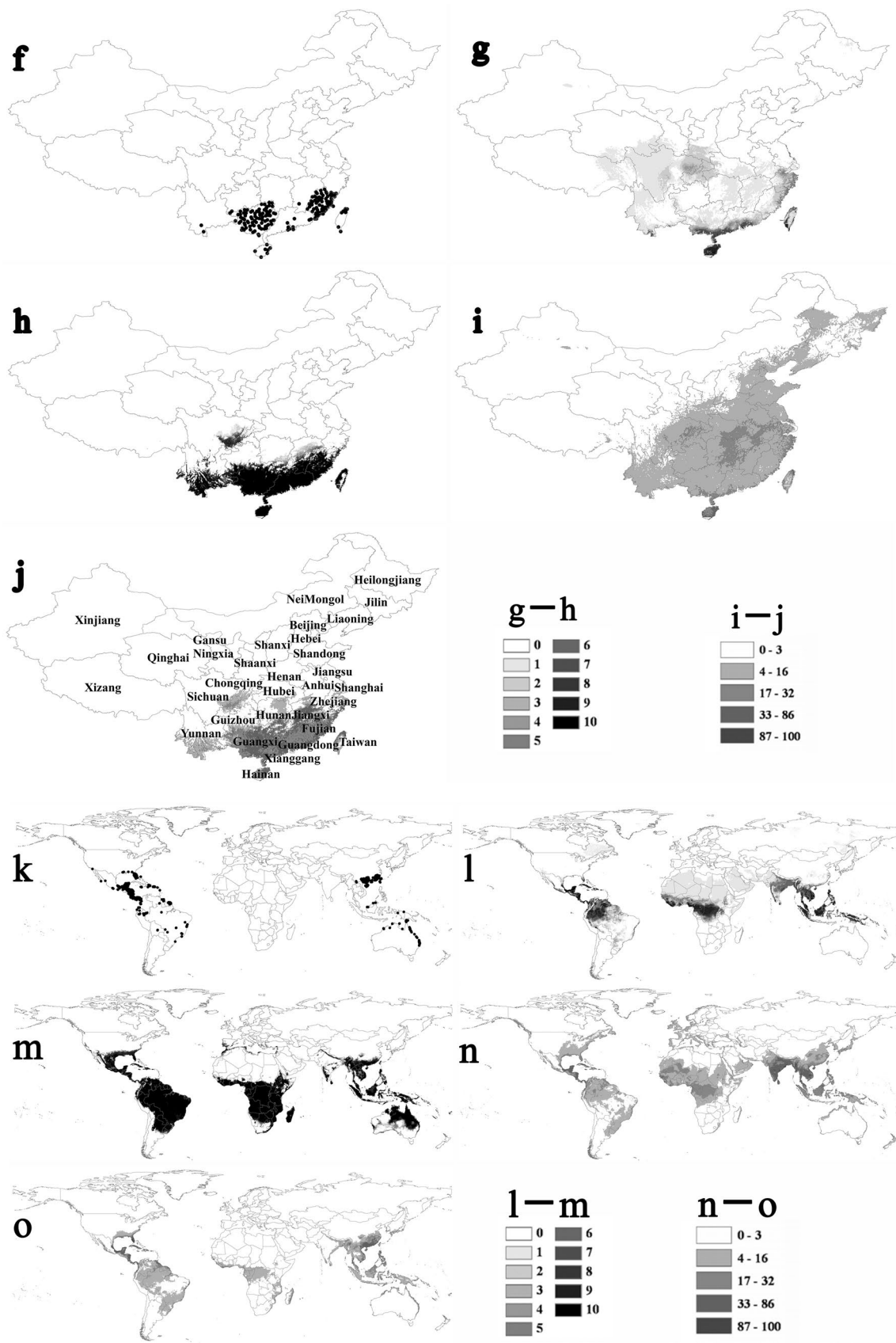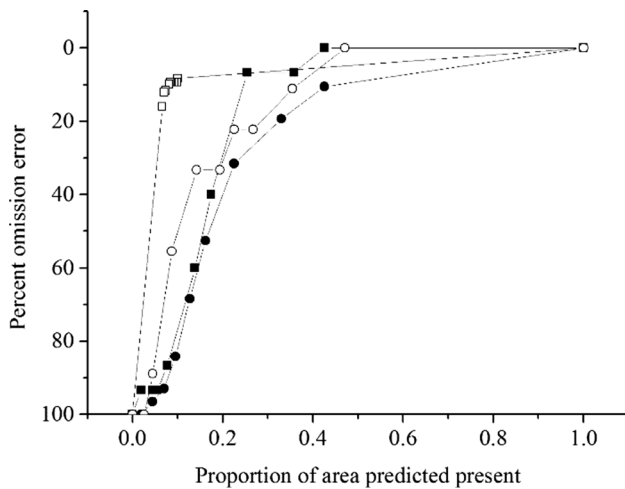
Fig. 3 continued

Fig. 4 Accumulation of predictive ability against proportion of area (China) predicted using GARP and Maxent models. *Filled and unfilled squares* represent GARP and Maxent full models, respectively. *Filled and unfilled circles* represent GARP and Maxent native models, respectively

North. The potential suitable area estimated by the GARP full model was 3.5 times that produced by the native model.

The Maxent full model predicted most known areas invaded by *W. trilobata* in China (Fig. 3). However, the model predicted small and scattered suitable areas consistent with the GARP full model, except for the Guizhou and Yunnan regions. The Maxent native model predicted extensive areas of China invaded by *W. trilobata* including northeastern regions. However, much smaller areas were identified by the Maxent models as potentially suitable for *W. trilobata,* confined mostly in the eastern and western regions of Hainan and Taiwan.

Global distribution of *W. trilobata*

Occurrences of *W. trilobata* in China were used to assess the predictive ability of the models to detect suitable areas for the species globally. Both GARP and Maxent model predictions were significantly better than expected under null models ($P < 0.0001$), indicating a reliable ability of the two approaches to predict the potential distribution of *W. trilobata* worldwide. Based on the full occurrence dataset, the two models performed better than models based only on native range points (Fig. 3). The GARP full model performed better at lower omission values while performance of the Maxent full model was better at middle and high level omission values (Fig. 4).

Global projections of the GARP and Maxent models indicated three geographically separate regions, namely the northern part of South America, mid-western Africa, and south and southeast Asia. The predicted distributional

maps of *W. trilobata* were generally consistent with current occurrence information from its native and non-native ranges. All the models identified various ranges vulnerable to colonization by *W. trilobata* in mid-western Africa, located around the Equatorial rain forest belt and East African coastal regions. The GARP full model predicted high suitability areas farther removed from the coast and areas extending more broadly southwards. This model also predicted high suitability in tropical South America and some bordering countries of Central and North America including Panama, Guatemala, Cuba, Dominican Republic and Mexico, a large southern part of Africa including Namibia, Angola, Zambia, Tanzania, Zaire, Congo, Uganda and West Tropical Africa (Guinea; Sierra Leone). Also predicted to have high suitability areas were northeastern Australia and southeastern Asia (especially Thailand, Cambodia, Vietnam, Malaysia and Indonesia), and some Pacific Island countries and territories (e.g. Fiji, Papua New Guinea, Federated States of Micronesia, New Caledonia). The main region where the GARP full model indicated broader potential distributional areas than the other models was in northeastern Australia. Compared with the full model, the GARP native model predicted distinct smaller range areas, especially in tropical South America. The model identified limited high suitability areas near the southwestern Equatorial rain forest belt, while detecting potential distribution areas north of the Equator (Fig. 3). The Maxent model projections yielded similar but more conservative predictions.

Discussion

Despite not including occurrence records from Africa for model generation, distributional ranges were successfully detected using the GARP and Maxent approaches. Observations and reports indicate that *W. trilobata* has been cultivated and become naturalized in parts of Africa including Benin, Congo Democratic Republic, Guinea, Mayotte, Sierra Leone, South Africa, and Zimbabwe (Hyde et al. 2014). In Zimbabwe, introduced *W. trilobata* plants have escaped from gardens and formed thick ground covers along the borders of plantations, roadsides and other disturbed areas (Henderson 2001). This species was observed thriving in high rainfall areas in the Eastern highlands and also in urban areas like Harare, which is characterized by a humid-subtropical mild summer climate. This climate is usually found in the highlands of some tropical countries (Köppen–Geiger classification: Cwb) (Kottek et al. 2006) including Mexico, Peru, and Bolivia. These climatic conditions are similar to conditions in the native range of *W. trilobata* and made it possible for this species to establish in Africa. Both the GARP and Maxent models make successful use of widely available environmental data to identify

suitable regions for the potential establishment of a species. These areas of suitability cannot be derived solely from the original occurrence dataset. Such regions of model 'over-prediction' having the potential to identify unknown distributional areas and unknown species have been demonstrated (e.g. Raxworthy et al. 2003). Additional research should focus on finding more effective ways (e.g. improve the transferability of the model by occurrence thinning or predictor selection) for projecting and interpreting the potential distribution of *W. trilobata.*

Performance of models

Using the GARP and Maxent models and based on native and full occurrence data points in this study resulted in a consistent distributional map for *W. trilobata*, although Maxent model findings were more conservative. The two modeling methods provided reliable predictions of the geographical extent of *W. trilobata* invasion using historical museum records which tend to be biased because they do not represent true absence values or guarantee that all areas have been adequately sampled (e.g. Anderson et al. 2003; Stockwell and Peterson 2003). When projected geographically to estimate the global distributional potential of the species, the GARP full model succeeded in predicting the known occurrences in Australia, while the Maxent models failed to identify the favorable habitats along the edges of invaded areas (e.g. Australia, Caribbean). This finding suggests that the GARP model based on the full range occurrences points may be able to better cope with spatial bias than Maxent models. As demonstrated, the GARP model does not respond to coordinate spacing, and might perform better in predicting distributions from incomplete coordinate sets (Costa and Schlupp 2010). The greater predictive capability of GARP models has been reported in other studies (Terribile and Diniz-Filho 2010; Townsend Peterson et al. 2007).

Despite most known occurrences falling within predicted areas, models based solely on native occurrences records were less effective in discriminating relative climate suitability. These native models also failed to capture habitats occupied by *W. trilobata* in Australia. One possible reason is that *W. trilobata* may occupy an environmental niche that is environmentally different from regions in its native range. Significant differences of the most important environmental variables between native and introduced *W. trilobata* ranges and results of principal components analysis on environmental layers indicates that this species may occupy distinct environmental niches in its invaded ranges. These differences and the ability of some plant species to rapidly evolve to adapt to a changing climate (i.e. environment) makes it especially challenging to predict the future geographic extent of plant species with models

using only native range data (Clements and DiTommaso 2011). In environmental space, the model identifies neither the occupied niche nor the fundamental niche (Hutchinson 1957) since the target species were unlikely to be at equilibrium and occurrence records will not completely reflect the full range of environmental conditions occupied by the species. Therefore, it would be more insightful to combine data from both the native and invaded ranges (e.g. Welk 2004). Because of potential niche shifts in a species such as *W. trilobata*, models based on data from both the invaded and native ranges may be more appropriate and insightful in determining its geographic range. As demonstrated in our study, models built on the full dataset can effectively predict the future spread of the species in areas that can be potentially invaded (Broennimann and Guisan 2008).

Potential distributions and environments

Both GARP and Maxent results indicated that *W. trilobata* can occur in areas with different environmental conditions than experienced in its native range. Using the updated Köppen–Geiger climate classification system (Kottek et al. 2006), most of the suitable areas susceptible to invasion by *W. trilobata* identified by these models fell within the Aw (tropical wet and dry or savanna climate) climate class. Other suitable regions prone to invasion included the Cfa or Cwa (the humid subtropical climate) classifications. The GARP full model also detected high suitability for invasion to some areas in the Af (tropical rainforest climate) and Am (tropical monsoon climate) climate classifications. These results confirm that *W. trilobata*, a tropical species prefers hot and humid environments. For example, *W. trilobata* colonized regions with temperate/mesothermal climates with dry winters (i.e. warm average temp. >10 °C, cold average temp. >0 °C, dry winters). Annual precipitation of suitable regions is typically high, although it does not have to be evenly distributed throughout the year. A good example of this suitability preference is southern China, a region generally classified as Cwa based on the Köppen climate classification system, and where *W. trilobata* is present year-round. In this region, average annual precipitation totals 1,652 mm with rainfall received mostly in the summer months when plant needs are greatest. Approximately 32.7 and 42.3 % of precipitation falls in warmest and wettest quarter of the year, respectively (Fig. 2).

The predicted distribution of *W. trilobata* provides evidence of the ability of this species to survive under a wide range of environmental conditions across numerous geographical regions. In its native range, *W. trilobata* occurs in habitats with tropical wet and warm winters. Outside of its native range as in China for example, *W. trilobata* has expanded into areas that have a wider range of monthly mean temperatures and narrower range of annual precipitation. These findings combined with plant traits that allow this species to adapt to

a wide range of environmental conditions including vegetative propagation (Wu et al. 2005), high photosynthetic activity (Song et al. 2010), allelopathic potential (e.g. Nie et al. 2004), and high energy-use efficiency (Song et al. 2009) are the main factors that may explain the success of *W. trilobata* to invade novel regions of the world. The models used in this study predicted regions of the world that are environmentally suitable for *W. trilobata* colonization, but they do not identify regions that will necessarily be invaded. The major reason for this difference is that our models did not account for barriers to seed dispersal, local soil or management factors, biotic interactions, and the capacity of species to adapt to new environments (Thuiller et al. 2008). Therefore, a comprehensive assessment of the invasion risk posed by this species indifferent regions of the world would require a more in depth understanding of the way that these barriers affect the population dynamics of the species (Thuiller et al. 2005).

Threat of *W. trilobata* invasion

Given the rapid spread of *W. trilobata* and serious risk this species may pose to resident ecosystems, efforts to limit its introduction and establishment in regions outside of its native range should be fully considered. For instance, *W. trilobata* was first introduced to South China in the 1970s as ornamental and has since become a major invasive weed. This plant is gaining increased popularity because it is an excellent ground cover and reduces soil erosion (Wu et al. 2005). Many Chinese farmers also believe that *W. trilobata* can be used in traditional medicine (Tsai et al. 2009). The GARP full model predictions showed that *W. trilobata* has the potential to expand its range along southeastern coastal areas and is able to extend into interior regions of eastern and southwestern China. More than 7 % of the study area was suitable for *W. trilobata* colonization under current environmental conditions. With development of a national horticultural industry and the fast growing ornamental trade sector in China, it is very likely that *W. trilobata* will quickly naturalize and invade regions of the country that are projected to experience increased temperatures in the coming decades. The deleterious effect of *W. trilobata* on native plant populations and biodiversity has raised concern in regions of China at higher risk of infestations because effective control strategies are not available in these areas. As a way forward, it is essential to identify and monitor areas most vulnerable to invasion by this aggressive plant, since early detection and rapid response will be crucial for minimizing economic losses and ecological damage. Practical management strategies are also needed in other regions of the world vulnerable to invasion by *W. trilobata* to meet conservation and biodiversity goals.

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