

# Predicting the spatial distribution of an invasive plant species (*Eupatorium adenophorum*) in China

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**Abstract** Invasive alien species can pose a severe threat to biodiversity and stability of the ecosystems they invade. Predicting distribution patterns of invasive species in regions outside their native range is a fundamental component of early warning systems. Crofton weed (*Eupatorium adenophorum* Spreng.) was first discovered in the Yunnan Province of China around the 1940s. The well-documented invasion history of this plant species provided the opportunity for us to examine the spatiotemporal patterns of biological invasion by crofton weed. Using the datasets documenting 441 known localities invaded by crofton weed in China over the past 50 years and 23 environmental variables generated by the genetic algorithm for rule-set production (GARP) model, we tested the predictability of crofton weed distribution with a high degree of accuracy. Both the Kappa statistics and the receiver-operator characteristic (ROC) analysis indicated that it is possible to predict the geographical spread of crofton weed in China. Precipitation in the coldest quarter of the year, extremely low air temperature, and maximum annual

air temperature strongly influenced the predictions. Our results indicate that crofton weed may break out in Yungui Plateau, Sichuan Basin, southeastern Coastlands, Hainan Island, and Taiwan although currently it is either absent or has only recently been recorded in these regions. Redundancy analysis (RDA) ordination results demonstrated that temperature and precipitation play an important role in confining the spread of crofton weed. Over the past 20 years, crofton weed has spread from subtropical areas with higher annual mean temperature and lower climatic fluctuations to much cooler and dryer areas at higher altitudes. The distribution of crofton weed was restricted mainly to regions with mean annual air temperature ranging from 10 to 22°C and annual precipitation from 800 to 2000 mm. Our results could help in developing and implementing early detection measures to minimize the ecological impacts of crofton weed invasion in China.

**Keywords** Geographic potential · Ecological niche modeling · *Eupatorium adenophorum* Spreng. · Spatiotemporal pattern · Biological invasions · China

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## Introduction

Biological invasion by alien plants has been identified as one of the most important contemporary ecological problems because of the potential threat it poses to biodiversity and stability of ecosystems (Wilcove

et al. 1998; Reichard and White 2003) and its adverse impacts on agricultural and forest productivity (Turpie et al. 2003; Knowler and Barbier 2005). Increasing global economic trade and trans-boundary activities make it almost impossible to avoid the spread of alien species across continents (McNeely 1999; Normile 2004) or the movement of species across different habitats within a region. Being able to understand the factors that regulate the spread of invasive species is an important goal of landscape ecology (With 2002). The ability to predict distribution patterns of invasive plants in regions outside their native range is fundamental to developing early detection systems and minimizing the ecological impacts of biological invasion by alien plants.

In China, a total of 108 plant species have been identified as alien weeds, of which 15 are distributed throughout most regions or the whole country (Qiang and Cao 2000). One of the most notable and noxious invasive alien plants is crofton weed (*Eupatorium adenophorum* Spreng.), a perennial herb native to Central America. It naturally spread into southern Yunnan province of China from Myanmar around the 1940s (Xie et al. 2001). The invasion of large areas of grassland and forest land by crofton weed has contributed to the decline in the numbers of indigenous animals and plants and decrease in biodiversity (Sun et al. 2004). Crofton weed is also a noxious plant known to cause acute asthma, diarrhea, depilation, and even death of livestock (Wu et al. 2004). The weed has invaded more than 30 countries including China, India, Thailand, New Zealand, Australia and the United States, resulting in extinction of many plants and severe economic losses (Fuller 1981; Wang et al. 1997). The ecological and socio-economic implications of biological invasion have prompted the urgent call for better methods to predict the areas where introduced species may become a threat (Rejmánek 2000; Welk et al. 2002; Richardson 2004).

Many different modeling approaches have been developed and used for predicting the likely distribution of plant species based on climatic and edaphic constraints (Segurado and Araújo 2004; Guisan and Thuiller 2005). One of the approaches that have proven to be especially useful is the genetic algorithm for rule-set production (GARP) modeling system (Peterson and Cohoon 1999). The GARP modeling approach employs four inferential sub-routines, namely atomic, BIOCLIM, range rules, and logistic

regression, in an iterative, artificial-intelligence-based system and uses raster-based environmental and biological data to produce a niche-based model of the environmental requirements of the given species (Stockwell and Noble 1992; Stockwell and Peters 1999). These models can then be projected onto other landscapes to predict the geographic distribution of species (Lim et al. 2002; Parra et al. 2004). By extrapolating the model to a region free from the species in question, the potential of that species to invade the region can be predicted (Peterson and Vieglais 2001). The predictive power of this approach has been well tested in applications such as biogeography and conservation (Ortega-Huerta and Peterson 2004; Araújo et al. 2005) and in assessing the effects of global climate change (Peterson et al. 2002; Parra-Olea et al. 2005).

Incomplete sampling and smaller populations are common problems in compiling or evaluating data on the distribution of alien species, particularly in the case of recently established species that are not yet to reach their limits of successful growth and reproduction imposed by climate. Stockwell and Peterson (2002) explored the sample size needed for accurate modeling via re-sampling of data for well-sampled species. But random re-sampling methods ignore the temporal correlations that may exist within real distribution data.

We used a 50-year chronological data set of crofton weed covering a large area of China, to build a more realistic scenario of typical early stages of crofton weed invasion, incorporated time series re-sampling as a historical simulation approach, modeled the fundamental niche of this species using the GARP approach, and analyzed the environmental parameters of known localities and within niche areas predicted as likely to be invaded by the weed. Our objectives were to (1) describe the spatiotemporal patterns of crofton weed invasion in China and (2) identify the regions vulnerable to invasion by crofton weed.

## Methods

### Datasets

Ecological niche models are based on non-random correlations between known occurrence of species and environmental datasets that describe parameters

related to the dimensions of the ecological niche of the species. To build models, environmental parameters of localities of known occurrence are determined and then used to identify geographic regions that have similar environmental parameters. Time series data are usually obtained by periodically re-sampling the target objects.

In our study, the occurrence of crofton weed was established for 441 localities using herbarium records in local and national museums throughout China and from literature and field investigations. The localities of known occurrence were then georeferenced using the *Electronic Sinomap* (2004). The dataset for predicting the distribution of the species consisted of dated crofton weed specimens from 1940 to 2003. Because there had been a marked increase in regionally clustered records as a result of systematically increased sampling efforts since 1990, we removed 20 records for the period 1990–2003 to compensate for any bias due to the increased sampling. A total of 390 historical records were selected and stratified, respectively in random and chronological order, into 39 sets of 10 records each as intrinsic training data in the modeling process. The prediction analysis began with the first set of 10 records, and successive sets of 10 records were added for each of the consecutive runs. The sequential addition of chronologically stratified data sets, which is a form of quasi-retrospective sampling, constitutes the temporal dimension of the dataset compared with randomly arrayed datasets to examine the influence of invasion time on the model performance. An additional set of 51 records was used for evaluating the performance of GARP models as the extrinsic test data.

In the modeling process, 23 eco-geographic data layers were used for the initial assessments of ecological niche dimensions, including climate data (i.e. annual total radiation, maximum, minimum, mean, extreme high and extreme low annual air temperatures, relative humidity, mean annual precipitation, precipitation in the warmest and the coldest quarters, and precipitation in the wettest and the driest months) for the period 1971–2000 from Chinese Ecosystem Research Network dataset (<http://www.cern.ac.cn/0index/>); topographic and hydrologic data (i.e. elevation, slope, aspect, topographic index, flow accumulation, and flow direction) from the USGS's Hydro-1K dataset ([\[edcdaac.usgs.gov/gtopo30/hydro/\]\(http://edcdaac.usgs.gov/gtopo30/hydro/\)\); soil data \(i.e. soil pH, soil moisture, and soil carbon\) from the IGBP-DIS dataset \(<http://www.sage.wisc.edu/atlas/>\) and soil units from the Global Ecosystems Database \(<http://www.ngdc.noaa.gov/seg/ecosys/ecosys.shtml/>\); and land cover classification based on AVHRR satellite imagery for 1992–1993 from University of Maryland Global Land Cover Facility \(<http://glcf.umiacs.umd.edu/index.shtml/>\). The coverage was limited to 2–54°N latitude and 73–136°E longitude, which was re-sampled to 1-km grid resolution. We used a jackknife manipulation and analysis and inspection of omission statistics to reduce the original sets of environmental layers to 17 ecological dimensions \(Peterson and Cohoon 1999\).](http://</a></p></div><div data-bbox=)

#### Niche modeling

The GARP method (<http://www.lifemapper.org/desktopgarp/>) works as an iterative process of rule selection, evaluation, testing, and incorporation or rejection to produce a heterogeneous rule-set describing the species' ecological niche. The general approach is described in greater detail by Fera and Peterson (2002). For each of the time-series dataset model runs, rules were generated for 1000 iterations and repeated 100 times using a differential data ratio of 80:20 for training and rule-set validation. We selected the 10 best-subset models out of the 100 replicates based on optimal combinations of error components (Anderson et al. 2003). The intersection of all the 10 best-subset models generated a final map with values ranging from 0 to 1 (1 for regions where all the models predicted niche presence; 0 for regions of niche absence). The resulting value (hereafter referred to as overlap index, OI) is interpreted as a measure of relative likelihood of correctly predicting the niche presence for crofton weed.

#### Test approach

To test our model predictions, the extrinsic test data were overlaid on the mosaic of models and evaluated through Kappa analysis (Cohen 1960) and receiver-operator characteristic (ROC) analysis (Hanley and McNeil 1982) as more reliable measurements, (Pearce and Ferrier 2000; Manel et al. 2001) advocated

by some researchers (Cumming 2000; McPherson et al. 2004). The Kappa statistic is a reliability metric that uses the classification probabilities of the model and of reality to compute the likelihood of agreement by chance. In other words, the Kappa value is useful for testing the null hypothesis that there is no more agreement than might occur by chance alone. Monserud and Leemans (1992) have suggested the following ranges of agreement for the Kappa statistic: poor,  $K < 0.4$ ; moderate,  $0.4 < K < 0.55$ ; good,  $0.55 < K < 0.85$ ; excellent,  $0.85 < K < 0.99$ ; and perfect,  $0.99 < K < 1.00$ . Unfortunately, the calculation of Kappa values requires that probabilistic predictions of occurrence be divided into concrete predictions of absence or presence, based on a single, potentially arbitrary classification threshold.

The “area under the curve” (AUC) of the ROC plot, instead, is a threshold-independent measure of model accuracy, which juxtaposes correct and incorrect predictions over a range of thresholds. It ranges from 0 to 1, with a value larger than 0.50 indicating a better than random-event performance (Fielding and Bell 1997). Given the various advantages and disadvantages to using these different measures, we chose not to use any one single measure to assess model accuracy in our analyses.

### Model evaluation

The model was evaluated using two criteria: the influence of each environmental layer on the models’ prediction accuracy and the prediction performance related to increasing invasion time and data completeness.

To assess the influence of the environmental layers, 10 repeated runs of GARP modeling, each consisting of 100 iterations, were performed in which each of the 23 layers was sequentially eliminated from the analyses, which resulted in 10 prediction maps for each of the eliminations. These maps were overlaid to produce a composite map, with each pixel having a value between 0 and 10 that indicated the number of replicate model runs predicting the presence of the weed. These maps were further compared pixel by pixel with composite maps generated by GARP for all the 23 layers following the same procedures. The level of agreement between maps was analyzed by Kappa and ROC statistics.

To assess the prediction performance related to increasing invasion time and data completeness, we tested the 10 best models using the original extrinsic testing dataset segregated from the training datasets with random addition and chronological addition for the known localities of the species based on the two types of statistical analyses mentioned above.

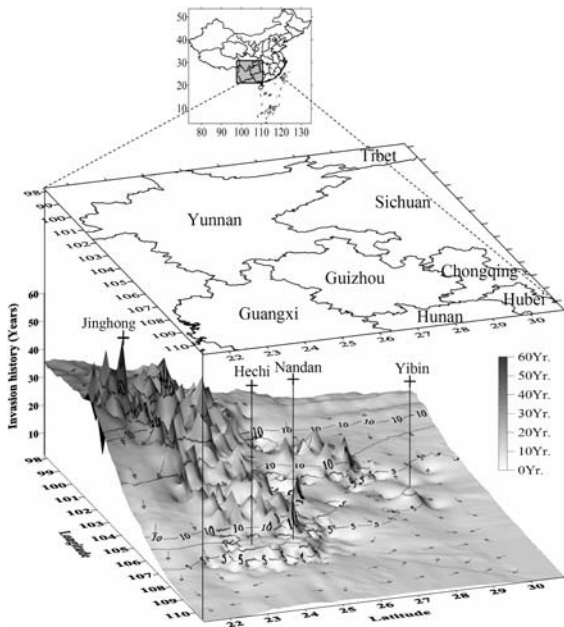
### Environmental envelope analysis

The zonal statistics routine (ArcMap 8.3, Spatial Analyst; ESRI 2003) was used to extract from the digital maps the values of 23 environmental variables in the localities where crofton weed is known to be present and in 1,000 random locations generated with a random point generator in ArcMap 8.3 (ESRI 2003). These values were used in the Redundancy Analysis (RDA; implemented in the software CANOCO 4.5; ter Braak and Šmilauer 2002) to order the invasion probabilities and spreading dynamics of crofton weed along the given environmental gradients. The significant environmental variables ( $P < 0.05$ ) were selected after a forward selection using an unrestricted Monte Carlo permutation test based on 9,999 random permutations.

## Results

### Spatiotemporal trends

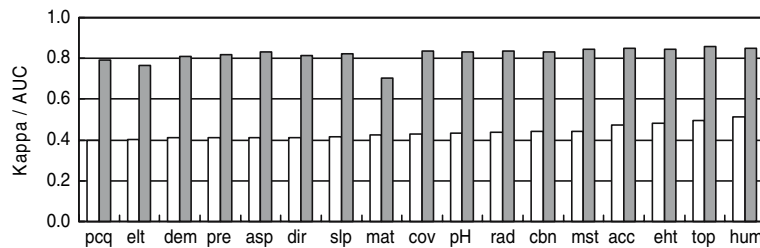
The chronological development and spatial autocorrelation for the locations of occurrence of crofton weed within the invasion time series illustrated a general trend despite the occurrence of numerous new records in the areas that were first invaded (Fig. 1). Crofton weed populations in China tended to be more recent towards the northern and southern limits of their distribution range. In the initial phase of the invasion, the range was limited to several isolated locations centered on the Jinghong region (Yunnan). Subsequently, the weed continued to expand and established clusters of invasion foci. Over the last 60 years, this weed has spanned  $23.4^\circ$  of latitude and  $9.6^\circ$  of longitude. The locations along Yibin (Sichuan) and Nandan-Hechi area (Guangxi) appeared to spearhead a more recent movement of the species by providing nascent foci for further invasion to the north and the east.



**Fig. 1** Spatiotemporal trends in crofton weed (*Eupatorium adenophorum*) invasion in south-west China. Geographical distribution of training data was plotted on the bottom *x–y* axis. Invasion history of distribution points based on recording dates was plotted on the vertical axis. The *black lines* represent the equal invasion time and the *grey arrows* indicate the direction of spread. The boundaries of administrative regions are marked on the top plane

Tests of model performance

Each of the more important environmental layers can be identified by the lower agreement value of the statistics after the layer is excluded from the rest of



**Fig. 2** Identification of the influence of each environmental layer on the models’ prediction accuracy based on Kappa and AUC (area under curve) values calculated from jackknife experiments. Layers excluded from model building are listed on the horizontal axis. The white and grey bars represent Kappa and AUC values respectively. *pcq*: precipitation in the coldest quarter, *elt*: extreme low annual air temperature, *dem*:

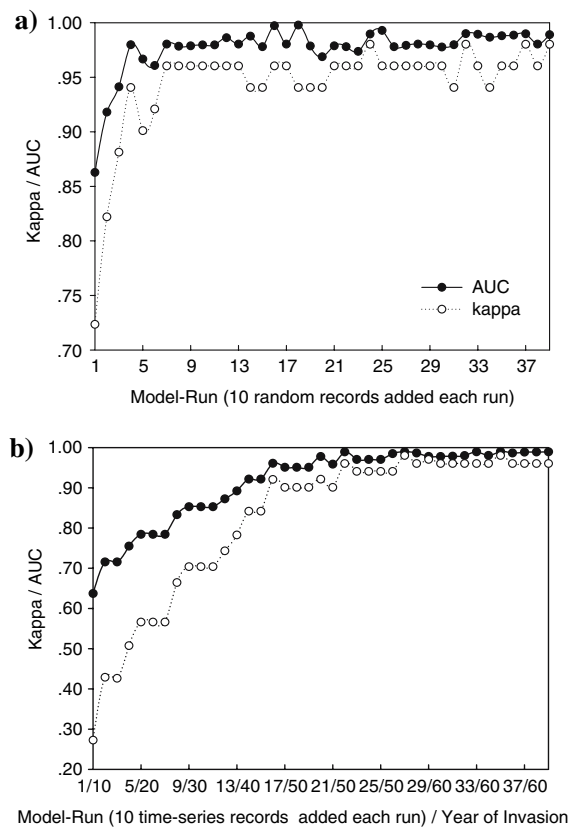
the layers using the jackknifing procedure (Fig. 2). The ROC analysis indicated that maximum mean annual air temperature, precipitation in the coldest quarter, and extreme low air temperature had the most influence on the predictions whereas the Kappa analysis identified only the latter two layers as the most influential factors.

As can be seen in Fig. 3, the predictive accuracy was related to sample size and especially to the spatial distribution of input data points. The curves of both Kappa and AUC values showed an increasing trend with the random and positive case addition until leveling off at the 7th run with 70 data points (Fig. 3a) and did not reach a steady state until the 22nd run with 220 data points in the time series (Fig. 3b) comprising 50 years of invasion history.

Predicted geographic distribution of crofton weed in China

The GARP analysis was based on a time series training set of 390 location records (Fig. 4). This analysis predicted a much wider distribution than current occurred areas for crofton weed extending to 192 counties and cities across seven provinces. Each of the 10 best-subset models from this analysis ( $\chi^2 = 217.99–331.56$ ;  $P < 0.001$ ) was imported into ArcMap (ESRI 2003) and displayed in geographic space as a mosaic of model intersections. Given that ecological niche models yield highly accurate predictions of the distribution of a species, the most likely areas for future invasion (i.e. OI = 1) include significant portions of Yunnan, Guizhou, Guangxi,

elevation, *pre*: mean annual precipitation, *asp*: aspect, *dir*: flow direction, *slp*: slope, *tmx*: maximum annual air temperature, *cov*: land cover, *pH*: soil pH, *rad*: annual total radiation, *cbn*: soil carbon, *mst*: soil moisture, *acc*: flow accumulation, *eht*: extreme high annual air temperature, *top*: topographic index, and *hum*: relative humidity



**Fig. 3** Quality assessments by Kappa and AUC values of the performance of the prediction model of modeling methods for under recorded or incompletely distributed items with random addition (a) and chronological addition (b). The larger value in this curve indicates greater reliability of the outputs of the corresponding model. The minimum sample size in this instance is just over 70 and the invasion records of at least 50 years are needed to attempt reliable prediction on a large-scale

Hainan, Chongqing, Hubei, eastern Sichuan, south-eastern boundary of Tibet, western Hunan, southern Shanxi; the coastal zone of Guangdong, Fujian, Taiwan, and Zhejiang; and isolated areas in Henan, Anhui, Jiangsu and Shandong.

Factors determining the invasion pattern of crofton weed across China

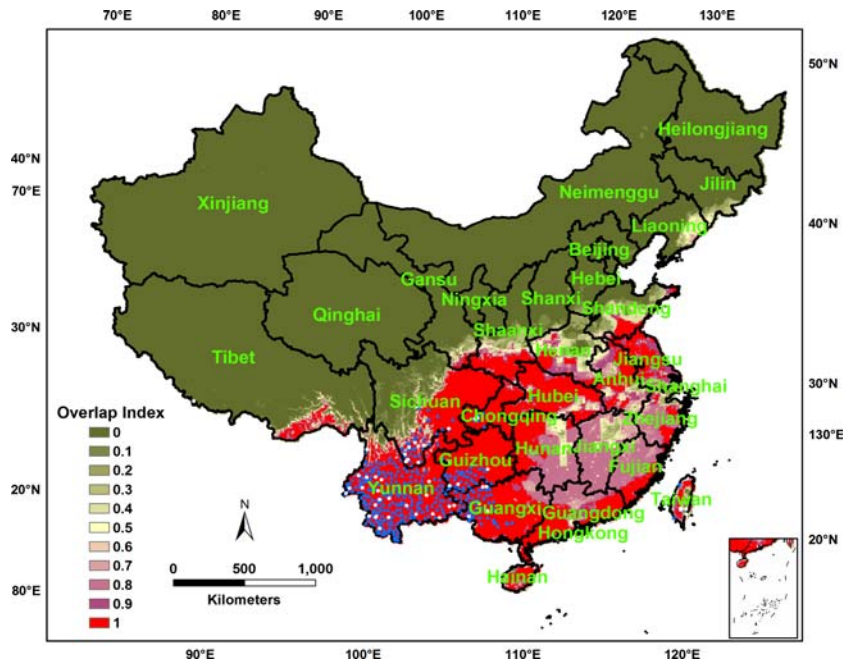
Figure 5a illustrates the relationships among the probabilities for crofton weed invasion and selected environmental parameters. The first two ordination axes explain 61.6% of the variation in distribution of the species and 97.7% of the variation in the relationship between the distribution of crofton weed and environment parameters respectively. An unre-

stricted Monte Carlo permutation test showed that the selected environmental variables significantly explained the total variance ( $P < 0.05$ ) as well as the variation along the first ordination axis ( $P < 0.05$ ). The first ordination axis is related mainly to extreme low, minimum, mean, and maximum annual air temperatures whereas much of the variance of the second ordination axis is explained by precipitation in the coldest quarter and mean annual precipitation. The higher OI values were associated with increased levels of moisture-related variables, especially mean annual precipitation and precipitation in the driest month. It can be inferred that both temperature and precipitation play a pivotal role in the spread of crofton weed to northern and eastern parts of China following the decrease in the value of OI. Figure 5b shows the relationships among the invasion dynamics of crofton weed and selected environmental parameters. In early stages of the invasion, most of the likely localities are in the highlands (average altitude of about 1,300 m) except on steeply sloped terrain ( $>15^\circ$ ); the occurrence of crofton weed is positively correlated with precipitation and temperature. In the later stages of the invasion, the occurrences of crofton weed were correlated negatively with temperature and precipitation but positively with geographic and edaphic factors such as elevation, land cover, soil type, and soil pH. Over the past 20 years, crofton weed has spread from subtropical areas with higher annual mean temperature and lower climatic fluctuations to much steeper, cooler, and drier areas at higher elevations.

Visualization of ecological niches

A graphical display of the pattern of crofton weed distribution influenced by concrete, tangible ecological parameters provides fertile ground for insights into the pattern of distribution. The known localities of crofton weed were well arranged (Fig. 6a) along the margin of predicted niches defined by the bivariate environmental space of mean annual air temperature and annual precipitation, with mean annual air temperature ranging from 4.4°C (Taoyuanlang in Taiwan) to 23.1°C (Taidong in Taiwan) and annual precipitation from 698 mm (Yuanmou in Yunnan) to 2254 mm (Jiangcheng in Yunnan).

The mean annual air temperature in the known localities (16.8°C; SD = 2.9) was above the average of



**Fig. 4** Geographic predictions for crofton weed (*Eupatorium adenophorum*) in China. Blue triangles represent the 390 spots used to train the predicted models and where the weed is known to occur, and white circles represent 51 extrinsic testing data used to test the predicted geographic range. To derive a robust result, all the available data (including extrinsic testing data) were used as input data in the final modeling after model

testing and validations. The different colors represent regions where crofton weed presence was predicted with varying degrees of certainty or likelihood (i.e. overlap index 1 means a higher possibility in that 10 out of 10 models predicted the presence; overlap index 0 means a lower possibility in that none of the 10 models did so)

that in randomly predicted locations (15.6°C; SD = 3.2) and the differences were significant (Mann-Whitney  $U = 68,284.5$ ,  $P < 0.001$ ), which indicated a trend for the spread of crofton weed toward locations with lower temperatures, whereas the mean annual precipitation in the known localities (1292 mm; SD = 252) was not significantly different from the average of that in randomly predicted presences (1326 mm; SD = 340; Mann-Whitney  $U = 84,019$ ,  $P = 0.244$ ). When temperature and precipitation in the sub-regions in which the presence of crofton weed was predicted were compared with those in which it was unlikely to spread, it became apparent that a broad combination of higher temperature and greater precipitation favored crofton weed. Within the regions of predicted presence, the majority of habitats had mean annual air temperatures between 10 and 22°C and mean annual precipitation between 800 and 2,000 mm.

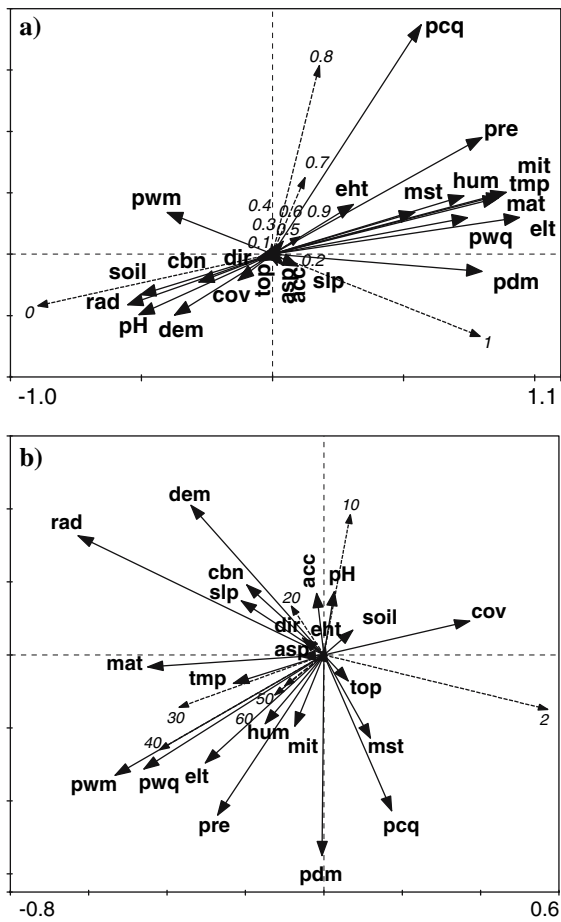
The predicted locations for continued invasion of crofton weed are characterized by lower values of extreme low temperatures and greater precipitation in

the coldest quarter of the year than in those locations where the invasion was held to be unlikely (Fig. 6b). Precipitation in the coldest quarter of the year for the predicted localities was also higher than that in the known localities of crofton weed, suggesting that crofton weed may be expected to spread further toward wetter regions.

## Discussion

Predictive power and practical consequences of the model

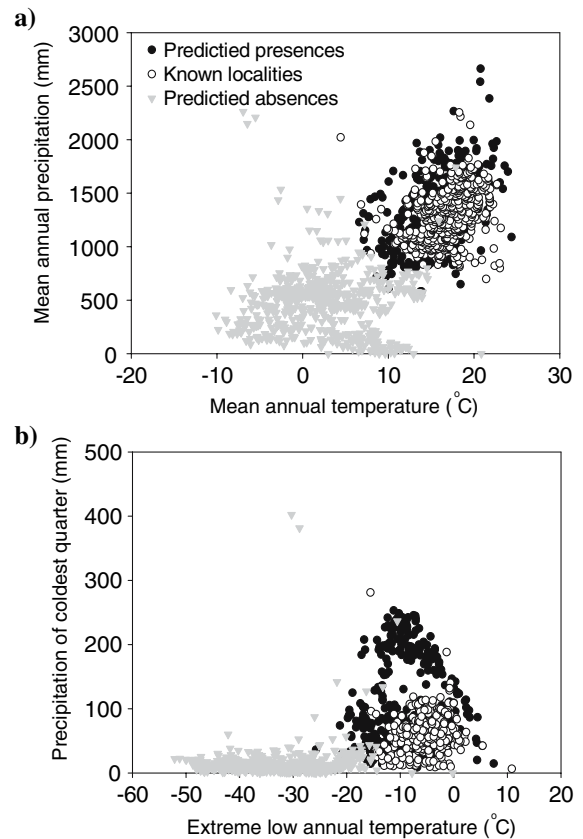
Hierarchical modeling schemes of environmental control on the spread of species, such as those discussed by Wu and David (2002), may be essential to the improvement of spatial modeling. In this study, however, we opted for the simpler niche modeling approach because our primary objective was not so much to eradicate the weed from localities where it is already established as to identify regions potentially



**Fig. 5** (a) Redundancy analysis (RDA) ordination diagram (showing first and second ordination axes) displaying the relation of crofton weed (*Eupatorium adenophorum*) invasion probabilities (arrows with dashed lines show OI value ranging from 0.1 to 1) and the correlation pattern of selected environmental characteristics (arrows with thick lines) in China. (b) RDA diagram displaying the relation of the temporal dynamics by crofton weed invasion (arrows with dashed lines show invasion years ranging from 2 to 60) and the correlation pattern of selected environmental characteristics (arrows with thick lines): tmn: minimum annual air temperature, tmp: mean annual air temperature, pwm: precipitation in the wettest month, pdm: precipitation in the driest month, pwq: precipitation in the warmest quarter and soil: soil category. For the explanations of the other abbreviations, see Fig. 2

vulnerable to invasion and implementing appropriate control measures. Our exercise proved effective in that it has achieved excellent predictive accuracy by identifying environmental parameters that influence the potential spread of the species.

In predicting new regions where a given species is likely to spread, the environmental conditions in the



**Fig. 6** Ecological niches of crofton weed (*Eupatorium adenophorum*) in environmental space. White circles indicate known localities; black dots and gray triangles indicate modeled predicted presences and absences, respectively, in the area of analysis

native range are often used as a constraint (Peterson et al. 2003; Iguchi et al. 2004). In this study, our predictions used the data on occurrence of the species in China. Although crofton weed has existed in China for about 60 years, it continues to expand its' range. Our datasets reflected the geographical non-equilibrium in the distribution of the species. However, given the long invasion history and diverse environmental conditions across the invaded regions, crofton weed can be considered to have occupied extremes of ecological niches in China. For many plant species, the current environmental conditions in their native ranges may not be necessarily consistent with the ecophysiological characteristics of the species (Hawkins and Sweet 1989; Sun and Sweet 1996). The distribution of a plant species reflects to a large extent the influences of a suite of factors related to evolution



and geological history of habitats and may not always fit the most suitable environmental conditions.

Papes et al. (2003) predicted the distribution of crofton weed in China based on environmental conditions in the native habitats and suggested that the species would occur mainly in eastern Yunnan, and central and south-eastern China. Our results, based on the locations in China where it has invaded and become established, seemed to fit the known localities better, which allowed for considering the possibility of changed niches regulated by different biotic (e.g. competitive exclusion) and abiotic factors (e.g. habitat specificities) (Davis et al. 1998) than in its' natural range. Certainly, to achieve more reliable spatial predictions over a shorter time span, distributional data in the native range should be incorporated into such models.

Spatial models of species distribution are commonly subject to two types of errors: errors of omission (exclusion of regions inhabited) and errors of commission (inclusion of regions not actually inhabited) (Fielding and Bell 1997). Insufficient sampling and ignoring the potential of non-equilibrium invasion would tend to increase the first type of error, leading to predicted values being lower than the actual values. Additionally, failure to take into account interactions among species (i.e., mutualism, competition, and predation), long distance dispersal, propagule pressure (Rouget and Richardson 2003), anthropogenic disturbance, and other restricting factors could lead to a gap between real and predicted distributions resulting from both types of errors. Approaches that take these processes into account will not only result in more accurate predictions but also provide better insight into specific factors controlling the distribution of invasive plants.

Despite the possible sources of errors, statistical analysis of our results indicated that our niche model based on records where crofton weed has invaded China and a 50-year record of crofton weed invasion had a high degree of predictive power. It included most known localities for crofton weed, suggesting low omission errors. Ninety-six percent of known localities were predicted by all models (OI = 1). The high predictive power of distribution ranges from niche modeling is widely reported (Anderson 2003; Raxworthy et al. 2003). Although the large-scale and long-term prediction of establishment can be based on the characteristics of a species' native and invaded

range using climate-matching models, invasiveness and invasibility are mainly determined by additional processes that act on much smaller spatial scale (Williamson 1999, 2001).

#### Dispersal mode and invasion pattern of crofton weed

Baker (1986) noted that invasion occurs through two modes: the steady advance and the stratified diffusion models. Crofton weed has been expanding from the south-west boundaries of China to the southern and eastern provinces as scattered satellite populations from the original center of introduction followed by infilling of the gaps. These long-distance hops are characteristic of 'stratified diffusion', which is the most frequent pattern of plant invasions such as that observed in the post-glacial dispersal of oak trees in Great Britain (Hengeveld 1989). The extent to which species spread by stratified diffusion may influence the choice of control strategies. For example, control measures that prevent the establishment of new foci or eliminate newly established foci are far more effective than those in which efforts are concentrated on invasion fronts already established (Moody and Mack 1988). As demonstrated in this study, the establishment of new foci through jump dispersal resulting from a heterogeneous landscape is of paramount importance in the spread of crofton weed.

Identification of factors that affect patterns and processes of the spread of species and potentially enhance or hamper species invasion is expected to suggest ways for effectively managing invasive species (Sakai et al. 2001; Fagan et al. 2002). The RDA analyses revealed that environmental characteristics are the key features determining the invasion patterns of crofton weed and provided justification for using environmental data in niche visualization. The occurrence of crofton weed was found to be positively correlated with precipitation and temperature and was more likely in regions with sufficient rainfall and higher temperatures. The predicted northern limit is 33.5°N corresponding to 0 °C isotherm in the coldest month in China. This temperature may represent a particular threshold for the weed to adapt to cold climates. Elevation and slope, despite having no direct biological effects on plants (Austin 2002), can influence crofton weed invasion through their

correlation with temperature and precipitation. The preference of crofton weed to highlands largely reflects their range in their native habitats (Lu and Ma 2004); most of their known localities occur at flatter, mid-elevation sites where soil moisture is relatively high. Those known localities may also represent staging areas where the weed could slowly adapt to an environment of steeper slopes and higher elevations.

The spread of crofton weed in China is far from over. Human transformation of landscapes has facilitated the dispersal of a species that already has strong reproductive capacity and long-distance dispersal capability (Wang et al. 1994). In south-western China, crofton weed is often found along major river systems such as the Jinsha, Yalong, Hong and Lancang, with the highest densities along river valleys, in riparian areas, and on riverine beaches. Hence, rivers may have been a major channel of spread for crofton weed. River corridors consist of an array of landscape elements (Ward et al. 2002) with a high frequency of open ground for colonization (Malanson 1993), thus forming dispersal networks connecting different landscapes (Forman and Godron 1986) and serving as a dispersal vector for alien invasive organisms (Renöfält et al. 2005). Crofton weed is reported to have reached the Yangtze River in 2003 and may continue to spread eastward along the river course if not contained.

#### Remarks on invasion by crofton weed

Crofton weed, a species characteristic of warmer regions with a tropical climate, appears to tolerate a wide range of environmental conditions within tropical and subtropical regions. Our study suggested that Yungui Plateau, Sichuan Basin, south-eastern Coastlands, Hainan Island, and Taiwan might be at high risk of invasion by this weed although currently the weed is either altogether absent in these regions or recorded only recently from isolated locations.

Despite its already widespread occurrence, crofton weed may expand further into regions susceptible to its invasion. Identification of such sites would help in formulating measures to contain its spread. One area of particular concern is south-east China given the number of open ports, which makes it highly susceptible to the introduction of alien weeds through frequent trade.

At present, the invasion of crofton weed is so extensive that eradication would be extremely labor-intensive, and removal projects, although possible on local scales, will have to be accompanied by long-term management efforts. An important means of conserving native biodiversity is to be vigilant in preventing crofton weed from entering the vulnerable areas. Under those circumstances, long-term monitoring systems to provide early detection and strict quarantine measures to avoid anthropogenic spread of crofton weed would be a high priority for the management of crofton weed invasion. Our predictions of potential distribution of crofton weed can provide a strong basis for identifying areas where detection efforts would be most effective and beneficial.

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#### References

- Anderson RP (2003) Real vs. artefactual absences in species distributions: tests for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. *J Biogeogr* 30:591–605
- Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecol Model* 162:211–232
- Araújo MB, Thuiller W, Williams PH, Reginster I (2005) Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Glob Ecol Biogeogr* 14:17–30
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Model* 157:101–118
- Baker HG (1986) Patterns of plant invasion in North America. In: Mooney HA, Drake JA (eds) *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, Berlin, Germany, pp 44–57
- Cohen JA (1960) A coefficient of agreement for nominal scales. *Educ Psychol Meas* 20:37–46
- Cumming GS (2000) Using between-model comparisons to fine-tune linear models of species ranges. *J Biogeogr* 27:441–455
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S, (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786

- Electronic Sinomap (2004) Sinomaps Press, Beijing, China
- ESRI (2003) Arcview GIS, version 8.3. Environmental Systems Research Institute Inc., Redlands, CA, USA
- Fagan WF, Lewis MA, Neubert MG, van den Driessche P (2002) Invasion theory and biological control. *Ecol Lett* 5:148–157
- Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York, USA
- Feria ATP, Peterson AT (2002) Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. *Divers Distribut* 8:49–56
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49
- Fuller TC (1981) Introduction and spread of *Eupatorium adenophorum* in California. In: Vebkata RB (ed) Proceedings of the 8th Asian-Pacific Weed Science Society conference. The Organizing Committee eighth conference of Asian-Pacific Weed Society, Bangalore, India, pp 277–280
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Hanley JA, McNeil VJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143:29–36
- Hawkins BJ, Sweet GB (1989) Evolutionary interpretation of high temperature growth response in five New Zealand forest tree species. *New Zeal J Bot* 27:101–107
- Hengeveld R (1989) Dynamics of biological invasions. Chapman & Hall, London, UK, 160 pp
- Iguchi K, Matsuura K, McNyset K, Peterson AT, Scachetti-Pereira R, Powers KA, Vieglais DA, Wiley EO, Yodo T (2004) Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Trans Am Fish Soc* 133:845–854
- Knowler D, Barbier E (2005) Importing exotic plants and the risk of invasion: are market-based instruments adequate? *Ecol Econ* 52:341–354
- Lim BK, Peterson AT, Engstrom MD (2002) Robustness of ecological niche modeling algorithms for mammals in Guyana. *Biodivers Conserv* 11:1237–1246
- Lu ZJ, Ma KP (2004) The influence of topographical factors on the invasion of the alien species, *Eupatorium adenophorum*. *Acta Phytocool Sin* 28:761–767
- Malanson GP (1993) Riparian landscapes. Cambridge University Press, Cambridge, UK
- Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *J Appl Ecol* 38:921–931
- McNeely JA (1999) The great reshuffling: how alien species help feed the global economy. In: Sandlund OT, Schei PJ, Viken A (eds) Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht, the Netherlands, pp 11–31
- Mcpherson JM, Jetz W, Rogers DJ (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *J Appl Ecol* 41:811–823
- Monserud RA, Leemans R (1992) Comparing global vegetation maps with the Kappa statistic. *Ecol Model* 62:275–293
- Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. *J Appl Ecol* 25:1009–1021
- Normile D (2004) Expanding trade with China creates ecological backlash. *Science* 306:968–969
- Ortega-Huerta MA, Peterson AT (2004) Modelling spatial patterns of biodiversity for conservation prioritization in North-eastern Mexico. *Divers Distribut* 10:39–54
- Papes M, Peterson AT (2003) Predicting the potential invasive distribution for *Eupatorium adenophorum* Spreng. in China. *J Wuhan Bot Res* 21:137–142
- Parra JL, Graham CC, Freile JF (2004) Evaluating alternative data sets for ecological niche models of birds in the Andes. *Ecography* 27:350–360
- Parra-Olea G, Martínez-Meyer E, Pérez-Ponce de León G (2005) Forecasting climate change effects on salamander distribution in the highlands of Central Mexico. *Biotropica* 37:202–208
- Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol Model* 133:225–245
- Peterson AT, Cohoon KP (1999) Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecol Model* 117:159–164
- Peterson AT, Vieglais DA (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* 51:363–371
- Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* 416:626–629
- Peterson AT, Papes M, Kluza DA (2003) Predicting the potential invasive distributions of four alien plant species in North America. *Weed Sci* 51:863–868
- Qiang S, Cao XZ (2000) Survey and analysis of exotic weeds in China. *J Plant Resour Environ* 9:34–38
- Raxworthy CJ, Martínez-Meyer E, Horning N, Nussbaum RA, Schneider GE, Ortega-Huerta MA, Peterson AT (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature* 426:837–840
- Reichard SH, White P (2003) Invasion biology: an emerging field of study. *Ann MO Bot Gard* 90:64–66
- Rejmánek M (2000) Invasive plants: approaches and predictions. *Austral Ecol* 25:497–506
- Renöfält BM, Jansson R, Nilsson C (2005) Spatial patterns of plant invasiveness in a riparian corridor. *Landscape Ecol* 20:165–176
- Richardson DM (2004) Plant invasion ecology dispatches from the front line. *Divers Distribut* 10:315–319
- Rouget M, Richardson DM (2003) Inferring process from pattern in alien plant invasions: a semi-mechanistic model incorporating propagule pressure and environmental factors. *Am Nat* 164:713–724
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC et al (2001) The population biology of invasive species. *Annu Rev Ecol Syst* 32:305–332

- Segurado P, Araújo MB (2004) An evaluation of methods for modelling species distributions. *J Biogeogr* 31:1555–1568
- Stockwell DRB, Noble IR (1992) Introduction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Math Comput Simulat* 33:385–390
- Stockwell DRB, Peters D (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *Int J Geogr Inf Sci* 13:143–158
- Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. *Ecol Model* 148:1–13
- Sun OJ, Sweet GB (1996) Genotypic variation in light and temperature response of photosynthesis in *Nothofagus solandri* var. *cliffortioides* and *N. menziesii*. *Aust J Plant Physiol* 23:421–428
- Sun XY, Lu ZH, Sang WG (2004) Review on studies of *Eupatorium adenophorum*—an important invasive species in China. *J Forest Res* 15:319–322
- ter Braak C.J.F., Šmilauer P (2002) CANOCO reference manual and CanoDraw for windows user's guide: software for canonical community ordination (version 4.5). Micro-computer Power, Ithaca, NY, USA, 500 pp
- Turpie JK, Heydenrych BJ, Lamberth SJ (2003) Economic value of terrestrial and marine biodiversity in the Cape Floristic region: implications for defining effective and socially optimal conservation strategies. *Biol Conserv* 112:233–251
- Wang F, Summerell BA, Marshall DR, Auld BA (1997) Inoculum production of *Phaeoramularia*, a potential mycoherbicide for crofton weed. *Aust Plant Pathol* 26:173–178
- Wang HJ, He P, Ma JL (1994) An investigation and research report on the dissemination of *Ageratina adenophora* on rangeland areas in Liangshan District of Sichuan Province. *Grassland China* 1:62–64
- Ward JV, Tockner K, Arscott DB, Claret C (2002) Riverine landscape diversity. *Freshwater Biol* 47:517–539
- Welk E, Schubert K, Hoffmann MH (2002) Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. *Divers Distribut* 8:219–233
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States: assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. *Bioscience* 48:607–615
- Williamson M (1999) Invasions. *Ecography* 22:1–8
- Williamson M (2001) Can the impact of invasive plants be predicted? In: Brundu G, Brock J, Camarda I, Child L, Wades M (eds) *Plant invasions, species ecology and ecosystem management*. Backhuys Publishers, Leiden, pp 11–20
- With KA (2002) The landscape ecology of invasive spread. *Conserv Biol* 16:1192–1203
- Wu J, David JL (2002) A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. *Ecol Model* 153:7–26
- Wu ZH, Qin GL, Deng TJ (2004) Invasion and establishment of *Eupatorium adenophorum* (Spreng.) and its risk appraisal in some areas of Guangxi. *Southwest China J Agric Sci* 17:469–471
- Xie Y, Li ZY, Gregg WP, Li DM (2001) Invasive species in China - an overview. *Biodivers Conser* 10:1317–1341