

# Invasion dynamics and potential spread of the invasive alien plant species *Ageratina adenophora* (Asteraceae) in China

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## ABSTRACT

*Ageratina adenophora* (Sprengel) R. King & H. Robinson (= *Eupatorium adenophorum* Sprengel) is one of the worst invasive alien species in China. Since *A. adenophora* was first noticed in Yunnan Province of China in the 1940s, its rapid spread has caused an ecological problem in south-western China. Understanding its historical invasion pattern and its potential for further spread is needed to plan the management of the species. We reconstructed the historical process of its invasion and analysed its ecological preferences in the invaded region. After a lag phase of 20 years (1940–60), *A. adenophora* spread rapidly throughout the south and middle subtropical zones in Yunnan, Guizhou, Sichuan, and Guangxi, China, with an average expansion rate of 20 km per year. It spread relatively slowly in north subtropical areas, with an average expansion rate of 6.8 km per year. It has not established in warm temperate areas within the invaded regions. Although range expansion in Yunnan stopped after 1990, the expansion of its range into neighbouring provinces indicates that *A. adenophora* has not reached the full potential of its distribution and its range is still rapidly expanding within China. We applied ecological niche modelling (GARP — Genetic Algorithm for Rule-set Prediction) to predict potential invasion areas in mainland China on the basis of occurrence points within colonized areas where *A. adenophora* has reached equilibrium. The predictions, confirmed by the range of values of four key environmental parameters, generally match the parameters of the geography and ecology in the invaded region. Southern and south-central China have climatic conditions suggestive of a high potential for invasion by *A. adenophora*. Climatic conditions in northern and western China appear unsuitable for *A. adenophora*. Urgent measures should be taken to prevent this species from further spreading into the vast areas of potential habitat in southern and south-central China.

## Keywords

Biological invasions, invasive alien species, ecological niche modelling, expansion rate, historical reconstruction, potential invasion area.

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## INTRODUCTION

The invasive alien plant species *Ageratina adenophora* (Sprengel) R. King & H. Robinson (= *Eupatorium adenophorum* Sprengel), commonly known as Crofton weed, is native to Mexico, where it is a common weed (Cronk & Fuller, 1995). It was introduced from Mexico to Britain in 1826 as an ornamental plant (Cronk & Fuller, 1995). It later became invasive and rapidly spread in southern and south-eastern Asia, eastern Australia, New Zealand, and south-western Africa (Cronk & Fuller, 1995). Since *A. adenophora* arrived in Yunnan Province, China, from Myanmar in the 1940s, its rapid spread has caused ecological problems

in south-western China (Qiang, 1998). *Ageratina adenophora* has become one of the worst invasive alien species in China (Xie *et al.*, 2001). Local governments and land managers have made great efforts, using biological and chemical controls, in attempts to eradicate this invasive plant (He & Liang, 1988). Every effort, however, has ended in failure. *Ageratina adenophora* is seemingly expanding its range largely towards adjacent uninvaded regions, especially towards the vast area of southern and south-central China.

Most previous studies of *A. adenophora* in China have focused on its local pernicious effects and issues relating to chemical control (Xue *et al.*, 1979; Gao, 1981; Xu, 1983; Wu *et al.*, 1984; Xiang & Fan, 1984; Wang *et al.*, 1994; Zhou & Xie, 1999; Xia

*et al.*, 2002). Reports on its distribution are also general and qualitative (Liu *et al.*, 1985; Zhao & Ma, 1989; Peng, 1991; Xiang, 1991). Besides, it is suggested that *A. adenophora* has gone through a period of rapid spread and has nearly reached a balance in competition with local species and its dispersal ability is currently decreasing (unpublished reports from the Chinese central government). On the contrary, Papes and Peterson (2003) suggest that *A. adenophora* is spreading rapidly in China, which brings into question the appropriate strategies for managing the invasion. Floristic data not only provide information on changes in abundance of a species within an area, but also provides insights into its ecology during the invasion process (Liebhold *et al.*, 1992; Pyšek & Prach, 1995; Mandák & Pyšek, 1998; Mack, 2000). Since Yunnan is one of the richest region in species diversity in China, frequent explorations have been organized there since before the 1900s, first by French missionaries, then by European explorers and scientists, and then later by Chinese botanists. A large amount of data about the spread of *A. adenophora* into this area can be obtained from both herbarium records and government documents. Since Yunnan is ecologically heterogeneous, it can also be used as a natural experimental site for determining the ecological characteristics and habitat preferences of invasive alien species. *Ageratina adenophora* therefore represents a suitable subject for reconstructing the invasion and spread of an alien species, and for developing a model for predicting its potential invasion for further spread within China. Recently, biological invasions have been added to the list of important factors driving global change (Mack *et al.*, 2000; Kriticos *et al.*, 2003). Managers of biological invasions require a synoptic view of invasions as early as possible so that impact risks can be assessed (Kriticos *et al.*, 2003). There is an urgent need to predict the potential range of *A. adenophora* in China. This information will help policy makers to determine appropriate management strategies.

Although Papes and Peterson (2003) suggest that *A. adenophora* is spreading rapidly in China, their prediction of the potential area that *A. adenophora* will colonize in China is based on the occurrence of the species within its native range in Mexico. Large, already colonized areas in Yunnan, especially in south-western Yunnan, the earliest known area of establishment of *A. adenophora*, were not predicted to be highly suitable areas by their methods. The deficiencies may be due to the low number of occurrence points in Mexico and the lack of precise distributional data from China to test the accuracy of their model, as they themselves stated. Williamson (2001), however, suggested that predictions of the range of an introduced species into an area should be based on the range of the species in another invaded area rather than in the native area. Concerning this question, and because the Yunnan highland, with its heterogeneous environments, covers nearly all climatic conditions found in China and has good distributional data on *A. adenophora*, we have tried to apply GARP to predict the potential invasion area in China on the basis of occurrence points in Yunnan. The aim of this research was to first reconstruct the historical introduction of *A. adenophora* and to identify and determine the invasion and expansion phases over the past 60 years. We also compared the different expansion rates of *A. adenophora* in areas distinctly

different from each other in ecology and climate, with the aim of obtaining a better understanding of its geographical and ecological pattern of invasion and spread. Finally, based on ecological niche modelling combined with the geographical and ecological patterns revealed in the historical reconstruction of its invasion, we have tried to predict the potential invasion areas in mainland China. This combined approach not only demonstrates the ecological characteristics of *A. adenophora* within the invaded areas and provides a synoptic view of its likely further invasion in China, but also sheds light on developing an appropriate strategy for predicting the invasiveness of alien plant species in other parts of the world.

## METHODS

### Data sources

To reconstruct the historical invasion of *A. adenophora*, we conducted six field investigations from 1999 to 2004 in Yunnan, Sichuan, Chongqing, Guizhou, and Guangxi provinces, China (see Appendix S1 in Supplementary Material). During the investigations, we met with local government officials and related people to determine the historical distribution and then carried out surveys along rivers and roads where *A. adenophora* was mostly likely to be established. Additionally, we consulted unpublished and published data from investigative reports organized by the Chinese central and local governments, especially reports on invasive plants, rangelands, weeds, and regional agriculture (see Appendix S1 in Supplementary Material). We consulted specimens of *A. adenophora* in seven herbaria of China (see Appendix S1 in Supplementary Material). Each specimen was checked for correct identification, collection number, location and date, and habitat characteristics. Specimens with imprecise information were ignored. Published literature was also used in this research (Xue *et al.*, 1979; Gao, 1981; Xu, 1983; Wu *et al.*, 1984; Xiang & Fan, 1984; Liu *et al.*, 1985; He & Liang, 1988; Zhao & Ma, 1989; Peng, 1991; Xiang, 1991; Wang *et al.*, 1994; Qiang, 1998; Zhou & Xie, 1999; Xia *et al.*, 2002).

We utilized the data provided by the collectors to estimate the location of a collection to a precision of 0.01°. When the descriptions were imprecise, we used the latitude and longitude of the centre of the survey section, village, or town. When collectors and investigators provided the latitude and longitude from global positioning system (GPS) units, we used those data after checked for accuracy.

Herbarium records, investigative reports, and published literature provide clear evidence of the presence of a species at a given place and time. However, none of those sources gives an indication of how long a species was present in an area before it was collected. Herbarium records can provide a more accurate record of a species' occurrence at a given place and time. In the current work, we accepted the date of collection on the specimen label as the date when *A. adenophora* was present in a given area. We also accepted the publication date of each published work as the date on which *A. adenophora* was present in an area, unless specific dates for the fieldwork were given.

Finally, we sequentially eliminated all later collections from the location, village, or town, where *A. adenophora* had previously

recorded. Overall, 334 occurrence points in 182 counties, of which, 102 were obtained from field investigations, 63 from herbarium records, and 159 from investigative reports and published literature, were utilized to reconstruct the history of invasion.

### Reconstructing the historical invasion

A geographical information system (GIS) was used to map the invasion dynamics of *A. adenophora*. All georeferenced occurrence points were input into the digital map of China (1 : 1,000,000). We used the county as the spatial unit to illustrate the expansion progress of *A. adenophora* in China. The occurrence points and ranges during different periods were marked with different shapes and colours.

The expansion rates of alien species can be used to identify the different phases of invasion (Wade, 1997). As invasions advance from their starting point, they spread at radially symmetric rates (Hengeveld, 1989). However, barriers can constrain the spread in certain directions resulting in ranges of irregular shapes (Hengeveld, 1989). When the geographical distribution of an expanding population is highly asymmetric, the neighbourhood measurement of range expansion is more appropriate (Shigesada & Kawasaki, 1997). Since the range expansion of *A. adenophora* in China was highly asymmetric, neighbourhood measurement was used to estimate the expansion rate. Following Andow *et al.* (1993), we calculated the expansion rate for each sequential pair of geographical range boundaries by the average range increment in a local neighbourhood ( $\Delta r$ ) over the time ( $\Delta t$ ) and approximated the average range increment by  $\Delta r = [(\Delta r_{\min}^2 + \Delta r_{\max}^2)/2]^{1/2}$ , in which  $\Delta r_{\min}$  and  $\Delta r_{\max}$  were the minimum and maximum distances between the old geographical boundary and new boundary, respectively. We used the software ArcGIS 8.3 to calculate the minimum and maximum distances, respectively.

### Modelling the ecological niche of *Ageratina adenophora*

Ecological niche models were developed based on the georeferenced occurrence points of *A. adenophora* in Yunnan. Ecological niches were modelled using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Peters, 1999). GARP is designed to relate the ecological characteristics of the known occurrence points to those of the points randomly sampled from the rest of the study region, seeking to develop a series of decision rules that best summarize those factors associated with the species' presence. The decision rules can then be projected back onto the geography to predict the geographical distribution of the species (Stockwell & Peters, 1999).

In GARP, the occurrence points are divided twice, evenly into training and test data sets. An initial 50% of the data points are set aside for a completely independent test of the model quality (extrinsic test data). Of the remaining points, 50% are used for developing models (training data), and 50% are used for tests of the quality of the model internal to GARP (intrinsic test data). GARP works in an iterative process of rule selection, evaluation,

**Table 1** Description of environmental data layers

Description	Included
Elevation	√
Slope	
Aspect	
Frost days (annual means 1961–90)	
Annual precipitation (annual means 1961–90)	√
Solar radiation (annual means 1961–90)	
Maximum temperature (annual means 1961–90)	√
Minimum temperature (annual means 1961–90)	√
Mean annual temperature (annual means 1961–90)	
Water vapour pressure (annual means 1961–90)	√
Wet days (annual means 1961–90)	

Data layers included in the final analysis are indicated with an √.

testing, and incorporation or rejection. Within the GARP process, a method is first chosen from a set of possibilities (e.g. logistic regression, atomic rules, range rules, and negated range rules). It is applied to the training data, and a rule is developed or evolved. Predictive accuracy is then evaluated based on 1250 points resampled from the intrinsic test data and 1250 points sampled randomly from the study region as a whole. Rules may evolve by a number of means that mimic DNA evolution, i.e. point mutations, deletions, and crossing over, etc. The change in the predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence. GARP's predictive abilities have been tested and proven under diverse circumstances (Peterson & Cohoon, 1999; Peterson *et al.*, 1999, 2002, 2003; Peterson & Vieglais, 2001; Peterson, 2001; Anderson *et al.*, 2002; Oberhauser & Peterson, 2003; Rice *et al.*, 2003).

GARP modelling in this study was carried out on Desktop-GARP (<http://www.lifemapper.org/desktopgarp>). Desktop-GARP offers much improved flexibility in choice of predictive environmental data layers. Initially, we used 11 data layers (Table 1), which are available in the form of raster grids with 0.1° resolutions (<http://www.lifemapper.org/desktopgarp>).

To reduce environmental data layers to just those that provide the highest predictive accuracy, we used a jackknife analysis. We ran multiple iterations (1–10) of models omitting each data layer, or suites of data layers, systematically. We then calculated correlation between the inclusion or exclusion of each layer in the model (coded 1 s and 0 s) and the omission error (percentage of extrinsic test data not predicted as present). Positive correlations were considered indicative of detrimental contribution of a particular data layer to model quality, and such layers were removed from further analysis.

Each replicate model is different because of the random components of the GARP algorithm. To optimize model performance, we developed 100 replicate models of species' ecological niche based on the random 50–50 splits of available occurrence points in Yunnan. The 10 best models were selected from 100 replicate models according to the procedure developed by Anderson *et al.* (2003). The procedure is based on the observation

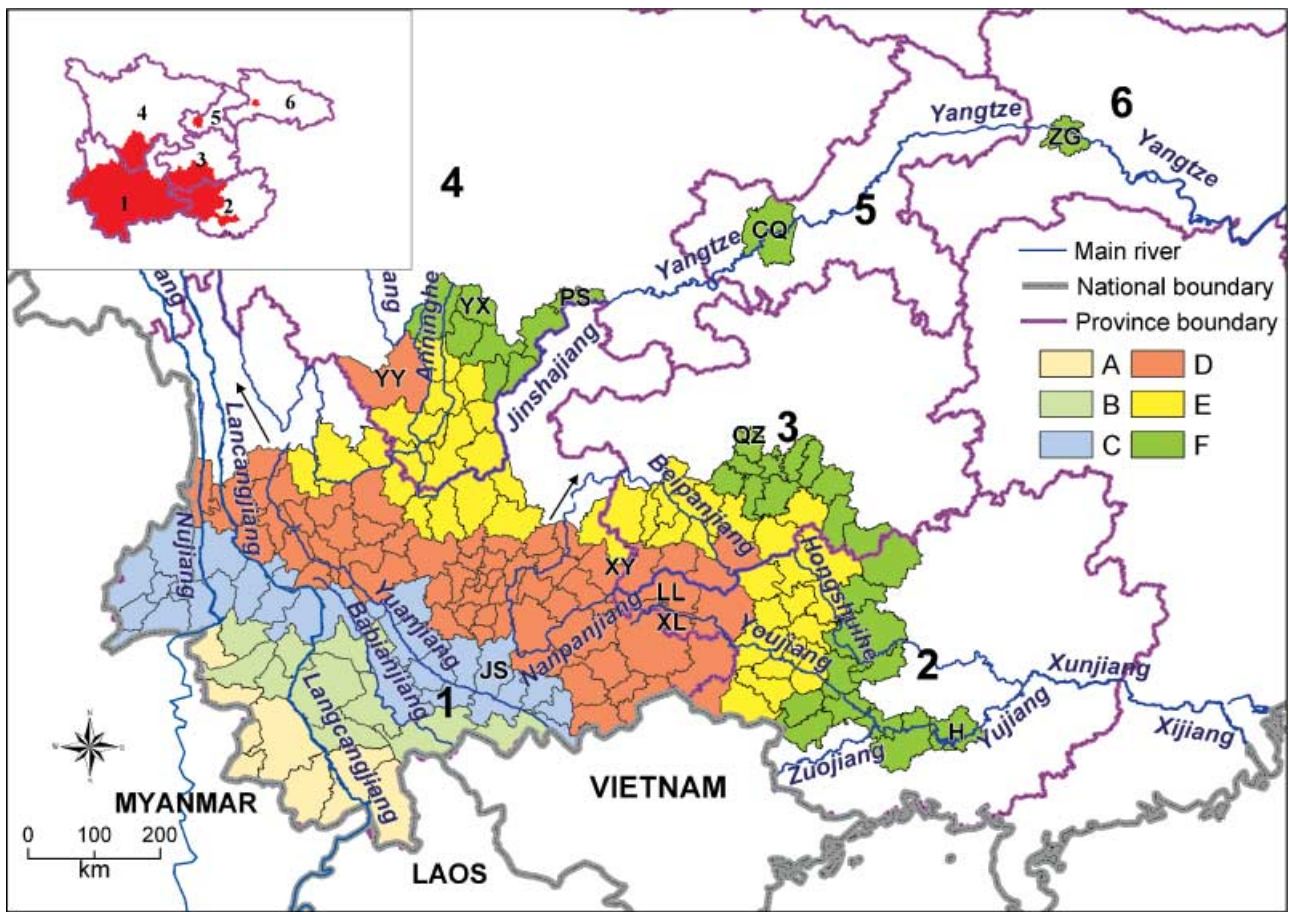


Figure 1 Historical and geographical expansion of *Ageratina adenophora* in China. Abbreviation: A, earliest invaded region; B, counties invaded before 1960; C, counties invaded in the 1960s; D, counties invaded in the 1970s; E, counties invaded in the 1980s; F, counties invaded > 1990; CQ, Chongqing City; H, Heng county; JS, Jianshui county; LL, Longlin county; PS, Pingshan county; QZ, Qingzhen county; XL, Xilin county; XY, Xingyi county; YY, Yanyuan county; ZG, Zigui county. Indication of number: 1, Yunnan Province; 2, Guangxi Province; 3, Guizhou Province; 4, Sichuan Province; 5, Chongqing City; 6, Hubei Province. The arrows (↑) indicate that *A. adenophora* stops spreading towards the north-east and north-west in Yunnan.

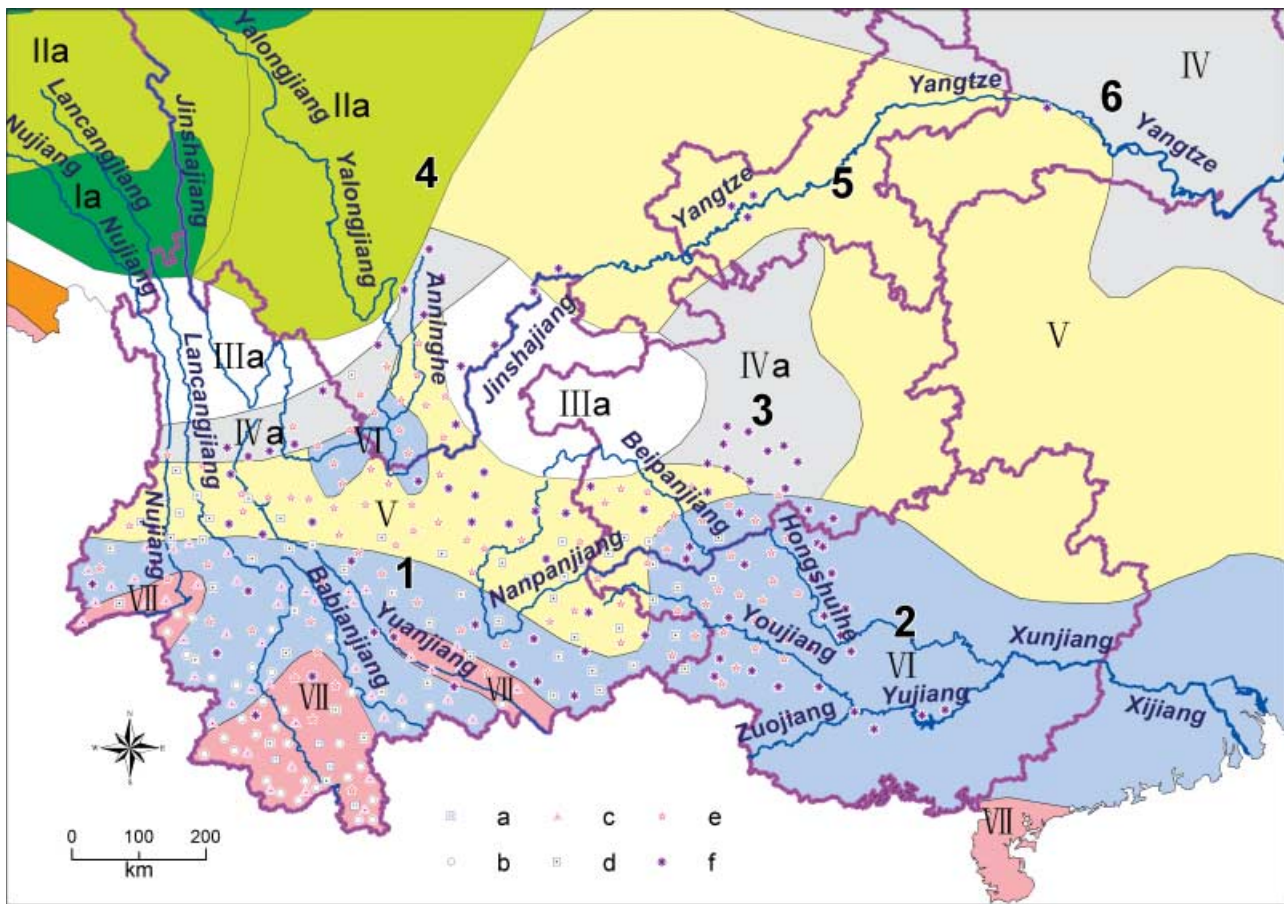
that (1) models vary in quality, (2) variation among models involves an inverse relationship between errors of omission (leaving out true distributional area) and errors of commission (including areas not actually inhabited), and (3) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points and moderate area predicted (an axis related directly to commission error). The relative position of the cloud of points relative to the two error axes provides an assessment of the relative accuracy of each model. Hence, to choose the best subsets of models, we (1) eliminated all models that had non-zero omission errors based on independent test points, (2) calculated the median area predicted present among these zero-omission models, and (3) identified 10 models that were closest to the overall median extent. ArcGIS 8.3 with the spatial analyst extension was used to integrate the output from 10 models. Each model was projected as a binary map (0 = areas of niche absence, 1 = presence). The 10 maps were added and then divided by 10 generating a final map with values ranging from 0 to 1 (1 for those regions where all the models predicted niche presence). The resulting value

(hereafter referred to as the overlap index, OI) is interpreted as a measure of the strength in the prediction of niche presence. Regions with high OI on the maps are those where confidence for the presence of *A. adenophora* niche is higher. Model quality was tested via the extrinsic test data. Chi-squared tests were used to compare the observed success in predicting the distribution of test points with that expected under a random model (the proportional area predicted to be present provides an estimate of occurrence points correctly predicted if the prediction is to be random with respect to the distribution of the test points) (Papes & Peterson, 2003; Peterson *et al.*, 2003).

## RESULTS

### Invasion and spread process of *Ageratina adenophora* in China

The invasion dynamics of *A. adenophora* in China were reconstructed based on data from field investigations, literature reports and herbarium specimens (Figs 1 & 2). Range expansion over



**Figure 2** Occurrence of *Ageratina adenophora* in different climatic zones. Abbreviation: a, earliest occurrence; b, occurrence before 1960; c, occurrence in the 1960s; d, occurrence in the 1970s; e, occurrence in the 1980s; f, occurrence after 1990. Indication of number: (see Fig. 1). Climatic zones and areas: IIIa, altitudinal warm temperate area; IV, north subtropical zone; IVa, altitudinal north subtropical area; V, middle subtropical zone; VI, south subtropical zone; VII, fringe tropical zone; Ia, altitudinal cool zone; IIa, altitudinal subcool zone. (Climatic regionalization data are cited from Zhang & Lin, 1985).

**Table 2** Some characteristics of the invasion process in different periods

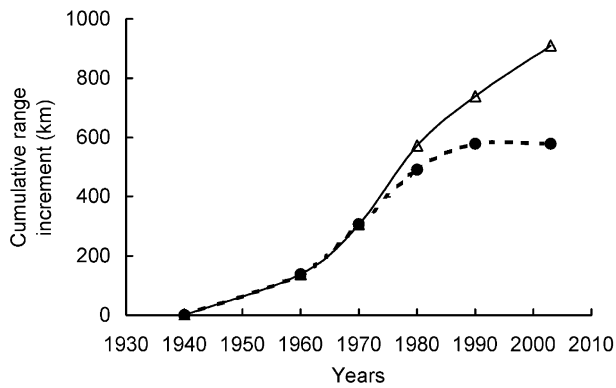
Five periods	Elevation range (m)	Climatic zone and area
Before 1960	500–1800	VII, VI
1961–70	500–2000	VI
1971–80	330–2300	VI, V
1981–90	500–2500	VI, V, IVa
1991–2003	500–2500	VI, V, IVa

Climatic zone and area: IVa, altitudinal north subtropical area; V, middle subtropical zone; VI, south subtropical zone; VII, fringe tropical zone.

60 years was divided primarily into five periods. Characteristics of the invasion process in different periods are shown in Table 2.

*Ageratina adenophora* was first noticed in Yunnan Province in the 1940s (Xie *et al.*, 2001). The earliest expansion of *A. adenophora* was limited to several counties along the border between China and Myanmar (Fig. 1). From these earliest observations,

*A. adenophora* spread northward and before 1960, *A. adenophora* was well established in southern Yunnan (Fig. 1). In the 1960s, *A. adenophora* began to rapidly spread to the north and east in southern Yunnan (Fig. 1). Most of the areas where *A. adenophora* was found were along the tributary streams and smaller tributary rivers of the Lancangjiang, Yuanjiang, Babianjiang, and Nujiang rivers (Fig. 1). By 1969, *A. adenophora* had been found over most of southern Yunnan (Fig. 1). In the 1970s, *A. adenophora* expanded its range largely in central and eastern Yunnan (Fig. 1). In the mid-1970s, *A. adenophora* spread from eastern Yunnan into Guizhou and Guangxi provinces (Fig. 1). In Guizhou Province, the earliest record of its occurrence was in Xingyi county (XY), from where it then spread northward, mainly along the Nanpanjiang river valley (Fig. 1). In Guangxi Province, *A. adenophora* first appeared in Xilin (XL) and Longlin (LL) counties, and then diffused eastward (Fig. 1). The early habitats were along the Youjiang river valley and its tributary streams (Fig. 1). Additionally, it also appeared in Yanyuan county (YY), Sichuan, north of Yunnan, in 1978 (Fig. 1). In the 1980s, *A. adenophora* nearly stopped its spread into north-west and north-east Yunnan (arrowhead) (Fig. 1), while it expanded rapidly into Sichuan,



**Figure 3** Cumulative range increments vs. years in south-western China (solid line) and Yunnan (dashed line).

Guizhou, and Guangxi (Fig. 1). The occurrence points of *A. adenophora* in the three provinces were mainly along river valleys and tributary streams, such as the Nanpanjiang river and Beipanjiang river in Guizhou, the Jinshajiang river and its tributary the Anninghe river in Sichuan, and the Youjiang river and Hongshuihe river and highways near those rivers in Guangxi (Fig. 1).

After 1990, *A. adenophora* spread in different directions in the above three provinces, while further extending its environmental preferences within the invaded parts of Yunnan (Fig. 1). By 2004, *A. adenophora* had covered most of Yunnan Province except some counties in the north-west and north-east regions (Fig. 1). In Sichuan Province, *A. adenophora* spread northward to Yuexi county (YX) located beside the Anninghe river and north-eastward to Pingshan county (PS) along the Jinshajiang river (Fig. 1). *Ageratina adenophora* was further found in Chongqing City (CQ) in 2002 and in Zigui county (ZG), Hubei in 2003 (Fig. 1). The two sites of invasion by *A. adenophora* are both along the Yangtze river. In Guizhou, it expanded to Qingzhen county (QZ) (Fig. 1) and in Guangxi it continued to spread eastward to Heng county (H) through which the Yujiang river runs (Fig. 1).

The region of invasion by *A. adenophora* in China is mainly along the fringe of the tropical zone (VII), the south and middle subtropical zones (VI,V), and the altitudinal north subtropical area (IVa) (Altitudinal variations in south-western China have a significant impact on the local climate, resulting in the climatic types correspondent with elevation. This type of climate is called altitudinal climate here, such as altitudinal north subtropical area that is similar to the climatic conditions of north subtropical zone in the latitudinal climate with variation as the latitude increasing from south to north.) (Fig. 2). Altitudinal north subtropical areas (IVa) are isolated in north-western Yunnan and central Guizhou (Fig. 2). Since *A. adenophora* first arrived in north-western Yunnan in the 1970s, it has spread at an average of 3.7 km per year. In central Guizhou, since its arrival after 1990, *A. adenophora* has spread at a low expansion rate of 9.8 km per year. The average expansion rate has been 6.8 km per year in the altitudinal north subtropical areas. There have been no occurrences of *A. adenophora* in regions that belong to the altitudinal warm temperate area (IIIa), except for some occurrences along the Jinshajiang-Yangtze river valley (Fig. 2). Elevations of the areas

where *A. adenophora* occurs range from 330 m to 2500 m (Table 2). The lowest elevation within the area of invasion is 330 m. Along the fringe of the tropics, *A. adenophora* mainly occurs at elevations greater than 500 m. Eighty-five percent of the occurrences range from 800 m to 2100 m (data not shown).

The spread of *A. adenophora* in China proceeded at different rates during different periods (Fig. 3). Before 1960, the expansion rate of *A. adenophora* was 5.8 km per year, but in the 1960s it accelerated to 16.8 km per year, and then reached 26.6 km per year in the 1970s. In the 1980s, the expansion rate was 16.6 km per year. The average expansion rate from 1960 to 1990 was 20 km per year. Even though the average expansion rate was 13.2 km per year after 1990, the expansion rate was 17.1 km per year along the Youjiang, Yujiang, and Hongshuihe rivers after 1990. Generally, the range of *A. adenophora* in China has continued to expand since it arrived in China (Fig. 3), but the range in Yunnan stopped increasing after 1990 (Fig. 3).

### Ecological niche modelling prediction

The jackknife analysis identified six environmental factors that were positively correlated with omission errors. Therefore, these six environmental factors detracted from the predictive abilities of the algorithm and were eliminated from final analysis (Table 1). The best prediction (i.e. zero omission error) was obtained using the remaining five environmental factors (Table 1). The 10 best subset models were highly statistically significant. The chi-squared tests, based on the independent extrinsic test data sets, indicated that the predictive ability of the 10 best subset models was far better than that of random models (all  $P \leq 1.5 \times 10^{-29}$ ).

The areas already occupied, except for several occurrence points between the Jinshajiang and Yalongjiang rivers, are predicted as having a high potential for invasion ( $OI \geq 0.7$ ) (Fig. 4). The subtropical zones (VI,V, IV) in southern and central China were predicted to be areas of the high potential invasion ( $OI \geq 0.7$ ) (Fig. 5). However, some southernmost regions in the south subtropical zone and some areas at low elevations at the fringe of the tropical zone were predicted to be lower potential invasion areas ( $OI \leq 0.3$ ) (Fig. 5). The altitudinal north subtropical area (IVa) in central Guizhou and part of the altitudinal warm temperate area (IIIa) in north-eastern Yunnan and western Guizhou isolated within the middle subtropical zone (V) were predicted to be areas of high potential for invasion ( $OI \geq 0.7$ ) (Figs 4 & 5). The altitudinal north subtropical area (IVa) and altitudinal warm temperate area (IIIa) in north-western Yunnan along the Nujiang, Lancangjiang, and Jinshajiang rivers were predicted to have lower potential for invasion ( $OI \leq 0.3$ ) (Figs 4 & 5). Northern and western China were predicted to have low potential for invasion ( $OI \leq 0.3$ ) (Fig. 5).

As stated above, jackknife analysis of the different environmental factors pointed to the critical role of minimum and maximum temperature, annual precipitation, and water vapour pressure in constituting the ecological niche of *A. adenophora* in China. To explore the role of these environmental parameters in influencing the invasion of *A. adenophora* in more detail, we

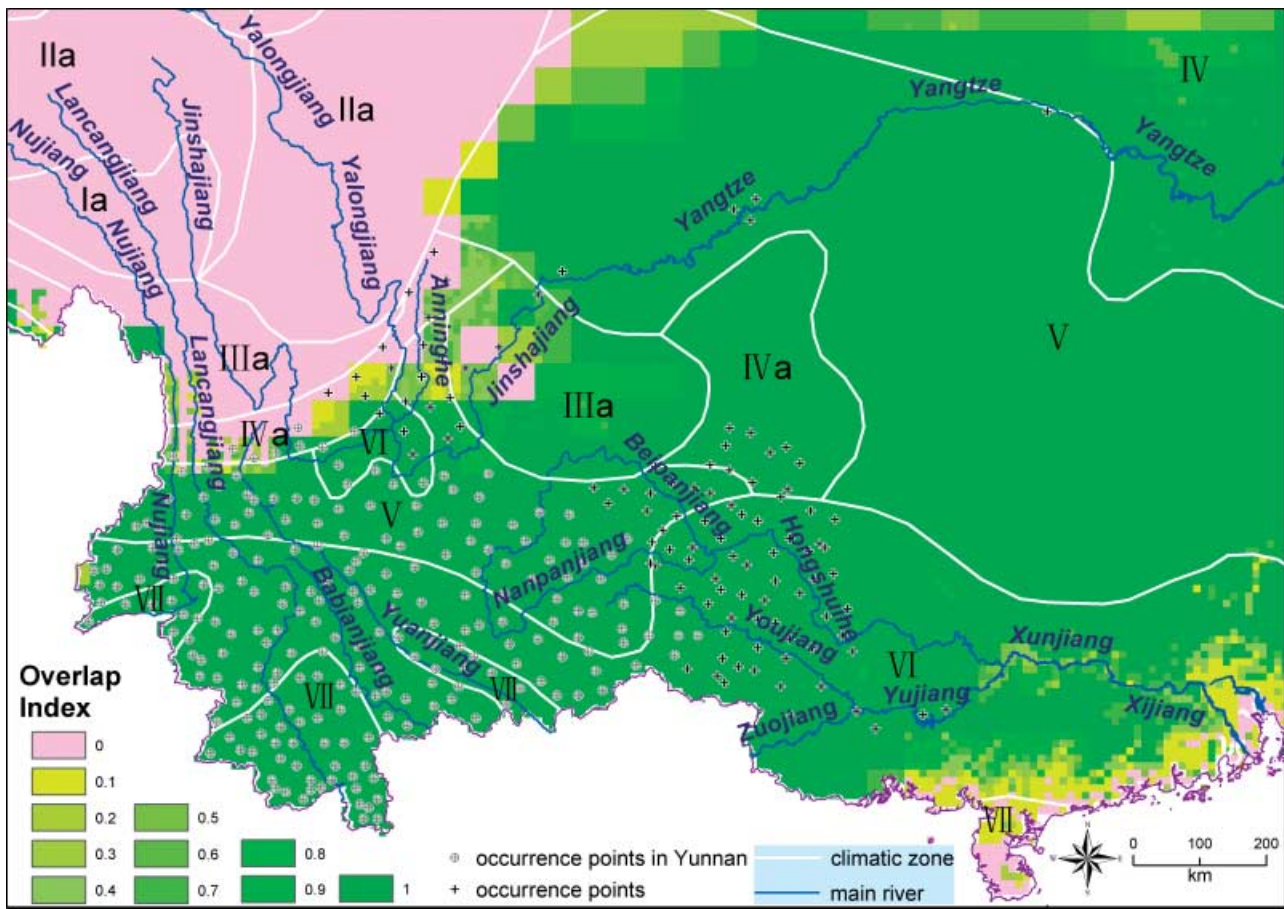


Figure 4 Map of the modelled potential distribution of *Ageratina adenophora* in south-western China. Greener regions are those where *A. adenophora* niche presence was predicted by more models (i.e. overlap index 1 means that 10 out of 10 models predicted presence, and overlap index 0 means that none of the 10 models did). Climatic zones and areas: (see Fig. 2).

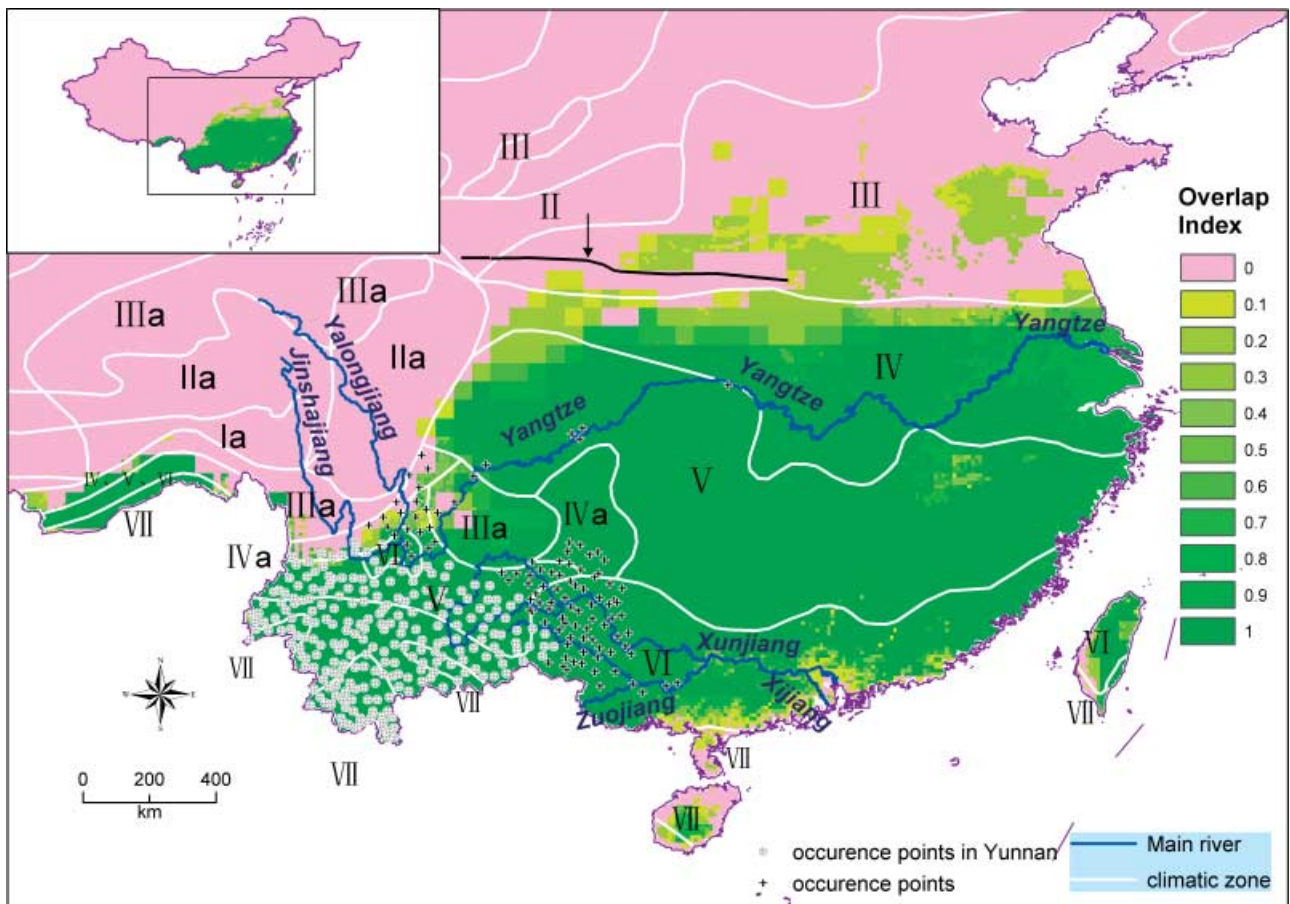
plotted the minimum temperature against the maximum temperature, and the water vapour pressure against the annual precipitation in the invaded areas, high potential areas, altitudinal warm temperate areas, and lower potential areas in northern, western, and southernmost China (Figs 6 & 7). In the invaded areas, the minimum temperature ranged from 9.7 °C to 19.5 °C, while the maximum temperature ranged from 18 °C to 30.5 °C. Annual precipitation ranged from 780 mm to 2240 mm, while water vapour pressure ranged from 1200 Pa to 2200 Pa (Figs 6 & 7). The ranges of the values of the four environmental parameters in the high potential invasion areas, i.e. in south and central China, were almost identical to those in the invaded areas (Figs 6 & 7). The values of the four environmental parameters in northern and western China predicted to have the lower potential for invasion were lower than those in the invaded areas, whereas the values of the four environmental parameters in southernmost China predicted to have lower potential were all higher than those in the invaded areas (Figs 6 & 7). The values of the four environmental parameters in the altitudinal warm temperate areas were just below or on the boundary between those in the invaded areas and in northern and western China (Figs 6 & 7).

## DISCUSSION

### Historical analysis of the invasion and spread of *Ageratina adenophora*

The earliest occurrence points of *A. adenophora* in China were mostly along the Lancangjiang river and its tributaries in the border region between China and Myanmar (Figs 1 & 2). During its spread in south-western China, the primary invasion sites were usually along rivers and highways adjacent to rivers. After its initial spread, *A. adenophora* expanded its range also mainly along tributary streams and highways in river valleys. The data further confirm that river valleys and highway margins are the main routes for invasion by and spread of *A. adenophora* in China, as reported by Wang *et al.* (1994).

According to the classification of expansion patterns proposed by Williamson (1996) and Shigesada and Kawasaki (1997), the successful establishment of an alien species can be characterized as occurring in three phases; an initial establishment phase with little or no expansion, an expansion phase, and a final saturation phase. From 1940 to 1960, the range of *A. adenophora* in China expanded at a rate of 5.8 km per year, which is much less than the



**Figure 5** Map of the modelled potential distribution of *Ageratina adenophora* in China. Greener regions are those where *A. adenophora* niche presence was predicted by more models (i.e. overlap index 1 means that 10 out of 10 models predicted presence, and overlap index 0 means that none of the 10 models did). The arrowhead (↓) points to the Qinling mountain ranges. Climatic zones and areas: II, middle temperate zone; III, warm temperate zone; IIIa, altitudinal temperate zone; the others are the same as in Fig. 2.

rate of spread in more recent years (Fig. 4). The 1940–60 period can be classified as the arrival and establishment phase, i.e. lag phase (Kowarik, 1995; Crooks & Soulé, 1999; Parker *et al.*, 2003). From 1960 to 1990 the range of *A. adenophora* in Yunnan and neighbouring provinces expanded (Fig. 4) at a rate of 16.8 km per year in the 1960s, 26.6 km per year in the 1970s and 16.6 km per year in the 1980s, the figures of which are all much higher than during period from 1940 to 1960. The period from 1960 to 1990 was the rapid expansion phase of *A. adenophora* in China. Even though the average expansion rate decreased to 13.2 km per year, the range of invasion continued to steadily increase in south-western China after 1990 (Fig. 3). The spread of *A. adenophora* had therefore not reached equilibrium and the species is still in an expansion phase in China. In Yunnan, however, the spread of *A. adenophora* stopped after 1990 (Fig. 3), indicating that *A. adenophora* had reached equilibrium with the environment within Yunnan.

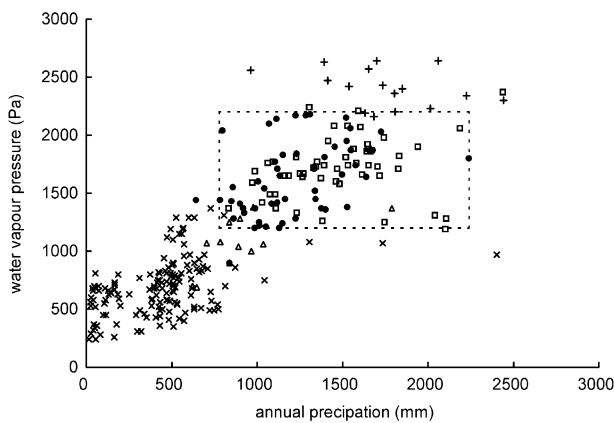
**Geographical and ecological pattern of its invasion and spread**

In eastern China, there are fringe tropical zone; south, middle, and north subtropical zones; and warm, middle, and cool

temperate zones from south to north (Fig. 5). Unlike eastern China, south-western China, especially Yunnan highland, has a complex and geologically young environment caused by the upthrust of the Himalayas as a result of the collision of the Indian subcontinent with mainland Asia about 50 million years ago (Sharma, 1984). This geographically and ecologically heterogeneous and variable environment has resulted in remarkably diverse climatic types, in which altitudinal and latitudinal climates are distributed in a mosaic pattern across large parts of Yunnan, Sichuan, Guangxi, and Guizhou (Fig. 2).

Altitudinal north subtropical areas (IVa) are isolated in north-western Yunnan and central Guizhou, respectively (Fig. 2). In north-western Yunnan, the altitudinal north subtropical area is located in the upper reaches of several rivers, i.e. Nujiang, Lancangjiang, Jinshajiang, and Anninghe rivers (Fig. 2), where the elevations range from 1700 m to 2100 m. Since *A. adenophora* first reached north-western Yunnan in the 1970s, it has spread at an average rate of 3.7 km per year, which is much lower than the average expansion rate of 18.8 km per year after 1970s. In central Guizhou, where the elevations exceed 1000 m, *A. adenophora* has spread at a low expansion rate of 9.8 km per year since it reached this area in the 1990s. In contrast, *A. adenophora* spread at a rate

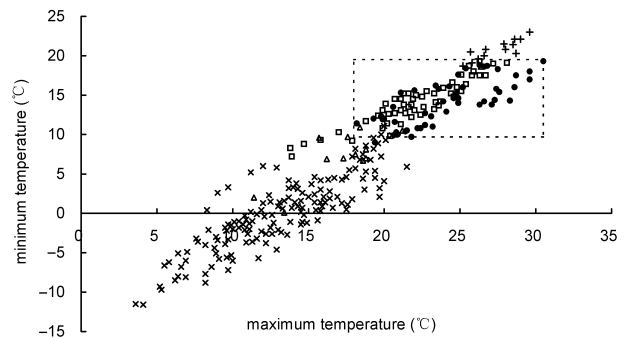




**Figure 6** Visualization of water vapour pressure against annual precipitation. Indication of signs: ●, the environmental conditions in the invaded area; □, the environmental conditions in the regions predicted to have high potential for invasion; △, the environmental conditions in the altitudinal warm temperate areas; ×, the environmental conditions in northern and western China predicted to have lower potential for invasion; +, the environmental condition in southernmost China predicted to have lower potential for invasion.

of 17.1 km per year after 1990 along the Youjiang, Yujiang, and Hongshuihe rivers with climatic conditions of south subtropical zone (Figs 1 & 2).

In the upper reaches of Nujiang and Lancangjiang above the altitudinal north subtropical area in north-western Yunnan, there is a distribution of the altitudinal warm temperate area (IIIa) with altitudes of more than 2100 m (Fig. 2). There has been no establishment of *A. adenophora* in this area to date. Another altitudinal warm temperate area is distributed in north-eastern Yunnan and western Guizhou with most altitudes of more than 1800 m surrounded by the altitudinal north subtropical areas (IVa) and middle subtropical zone (V) (Fig. 2). Except for several isolated occurrence points along the Jinshajiang-Yangtze river valley with a dry and hot microclimate below the altitude of 1000 m (Wu, 1980), *A. adenophora* has not been established in this altitudinal warm temperate area (Fig. 2). These altitudinal warm temperate areas are adjacent to the central plain of Yunnan, where *A. adenophora* rapidly spread during 1970s. However, *A. adenophora* almost stopped spreading forward in front of these altitudinal warm temperate areas after 1990. Therefore, it is difficult to geographically explain the non-establishment of *A. adenophora* in the altitudinal warm temperate areas. The values of the four environmental parameters in the altitudinal warm temperate areas were lower than in the invaded areas (Figs 6 & 7). It is most possible that the climatic and ecological conditions of warm temperate areas are unfavourable for the survival of *A. adenophora*. From the data above, *A. adenophora* has spread rapidly under the climatic condition of fringe tropical, south, and middle subtropical zones, while it expanded more slowly in cooler areas and in areas with a more pronounced seasonal climate and this will likely be the pattern until all areas with a similar climate are colonized.



**Figure 7** Visualization of minimum temperature against maximum temperature. Indication of signs: (see Fig. 6).

### Prediction of potential invasion regions in the mainland of China

As mentioned above, *A. adenophora* has not reached the full extent of its potential range in China. The distribution and range of climatic conditions suitable in its native range and in previously invaded regions provide indications of potentially suitable habitats for further colonization (Kriticos & Randall, 2001). A species with a certain impact in one place may have a similar impact in another place that is broadly similar ecologically, and is widely thought to be the best predictor (Williamson, 1996). To predict the potential distribution of a non-native species, it is necessary to analyse its current distribution and to determine its climatic and environmental requirements (Kriticos & Randall, 2001). The historical pattern of invasion and expansion under particular ecological and geographical conditions allows us to predict the potential invasion area of non-native plants, such as *A. adenophora*. Therefore, using GARP in combination with the geographical and ecological patterns revealed in reconstructing the history of invasions, we will try to predict the potential invasion area of *A. adenophora* in China.

The prediction by GARP generally matches the geographical and ecological pattern of the already colonized regions. The invaded areas, except for several spots between the Jinshajiang and Yalongjiang rivers are predicted to have high potential for invasion ( $OI \geq 0.7$ ) (Fig. 4). The uninvaded subtropical parts of southern and central China, especially in southern and south-central China, are predicted to have a high potential for invasion by *A. adenophora* ( $OI \geq 0.7$ ) (Fig. 5). The temperate zones of northern and western China are predicted as have lower potential for invasion ( $OI \leq 0.3$ ) (Fig. 5).

The vast uninvaded area of southern and south-central China, on the edge of the tropics (VII), and the south and middle subtropical zones (VI, V, IV) are predicted to have a high potential for invasion ( $OI \geq 0.7$ ) (Fig. 5). The ecosystem there has been even more seriously degraded by human activities than in the already invaded area with similar climatic conditions in Yunnan, Guizhou, and Guangxi (Wu, 1980). Additionally, *A. adenophora* has invaded some isolated spots along the Yangtze river in south-central China (Fig. 5) and is rapidly spreading eastward along the Youjiang, Yujiang, and Hongshuihe rivers into southern China.

Therefore, both predictions, using GARP and the pattern of invasion in the invaded areas, indicate that the vast subtropical region of southern and south-central China is most favourable for the invasion and spread of *A. adenophora*. Those areas are actually threatened because they are immediately adjacent to the invaded regions and have no geographical barriers to prevent the spread of *A. adenophora*. Some southernmost areas in the south subtropical zone (VI) and some areas with elevations below 300–500 m on the fringe of the tropics (VII), however, are predicted to have a lower potential for invasion by GARP ( $OI \leq 0.3$ ) (Fig. 5). This might be because in these regions the minimum temperature and water vapour pressure are higher than in areas suitable for *A. adenophora* to survive, as shown above (Figs 6 & 7).

GARP also predicted most of the north subtropical zone in central China to have a high potential for invasion ( $OI \geq 0.7$ ) except at the boundary between the subtropical and warm temperate zones (Fig. 5). Similarly, the altitudinal north subtropical area already invaded in central Guizhou was predicted to have a high potential for invasion ( $OI \geq 0.7$ ), whereas the altitudinal north subtropical area already invaded in north-western Yunnan was predicted to have a lower potential for invasion ( $OI \leq 0.3$ ) (Fig. 5). The expansion rate of 9.8 km per year by *A. adenophora* in central Guizhou is much higher than in north-western Yunnan, where it is 3.7 km per year. The values for the four environmental parameters in central Guizhou are also higher than in north-western Yunnan (data not shown). The different environmental conditions might be due to higher elevations in the north-western Yunnan where environmental conditions are transitional between subtropical and temperate areas. The scattered, already invaded spots in north-western Yunnan may have favourable microclimates, for they are usually located along rivers at lower elevations. The latitude–longitude resolution of the environmental data used in this research is  $0.1^\circ$ , which is insufficient to resolve microclimates. Additionally, even though the altitudinal north subtropical area in central Guizhou was recognized to have a high potential for invasion, the actual expansion rate there was much lower than in middle subtropical climates. These facts indicate that the north subtropical areas are transitional between the middle subtropical and warm temperate zones and are less favourable for the invasion and spread of *A. adenophora*.

It is also predicted that warm to cool temperate zones in northern and western China have a lower potential for invasion (Fig. 5). Geographical and ecological patterns revealed in the invasive historical reconstruction of *A. adenophora* indicate that the climatic and ecological conditions in the warm temperate area may be unsuitable for the survival of *A. adenophora*. The climatic and ecological conditions in northern and western China were much worse than in the altitudinal warm temperate area (Figs 6 & 7). In addition, the Qinling Mountain with altitudes of 2000–3000 m, which lies between the north subtropical zone (IV) and warm temperate zone (III), would be a geographical barrier for *A. adenophora* to spread to the uninvaded warm temperate zone in China (Fig. 5). Some of the uninvaded warm temperate areas in south-eastern Yunnan and western Guizhou predicted as the potential areas for invasion might be due to insufficient recognition under the  $0.1^\circ$  latitude–longitude resolution of

the environmental data. Because this region is nearly surrounded by *A. adenophora*, it is necessary to continue monitor the area.

Papes and Peterson (2003) applied GARP to predict the potential invasion areas of *A. adenophora* in China using the province as the spatial unit. Large parts of the invaded areas in China were not predicted to be highly suitable for *A. adenophora*. Additionally, most areas where *A. adenophora* is actually spreading in southern and south-central China were also not predicted to have a high potential for invasion. In contrast, some warm and middle temperate areas in northern China were predicted to have a high potential for invasion by Papes and Peterson (2003). Their prediction was developed based on occurrence points in Mexico, of which the number is low, as they themselves stated. The essence of GARP is development of an ecological niche model based on the ecological characteristics of the known occurrence of a species (Stockwell & Peters, 1999). The predictive accuracy is related to number of data points (Welk, 2004). Thus, the poor prediction by Papes and Peterson (2003) may be due to the low number of occurrence points in the native area and their lack of precise occurrence data in China, which limited their ability to test the accuracy of their model as they stated themselves. In the other respects, it would be true, as Williamson (2001) pointed out, that climatic predictions of the range of an invasive species in an area should be based on its range in another invaded area rather than on its area of nativity.

## CONCLUSIONS

In general, after a lag phase of 20 years from 1940 to 1960, *A. adenophora* rapidly expanded its range in Yunnan and neighbouring region, China, at an average expansion rate of 20 km per year under climatic conditions of south and middle subtropical zones. At the same time, it spread at an expansion rate of only 6.8 km per year in altitudinal north subtropical areas. There was no establishment in the altitudinal warm temperate areas in the invaded regions. Although the spread of *A. adenophora* in Yunnan stopped after 1990, range expansion into neighbouring provinces indicates that *A. adenophora* has not reached equilibrium with the potential environment for colonization and is still in a rapid expansion phase in China. The prediction of the potential area suitable for *A. adenophora* using ecological niche modelling generally matches the ecological parameters of *A. adenophora* in the invaded region. The climate of southern and south-central China is recognized as being highly suitable for *A. adenophora*. It is less likely to spread rapidly in central China because of unfavourable conditions. Northern and western China do not have suitable climatic conditions to allow its spread into those areas. Urgent measures should be taken to prevent the further spread of *A. adenophora* into the southern and south-central China. In addition, our prediction with combination of ecological niche modelling and the geographical and ecological pattern revealed in the historical reconstruction of its invasion further indicate that it seems more accurate and effective to develop an appropriate strategy for the prediction of the potential range of an invasive species based on the occurrence points within colonized area where it has reached equilibrium than on its area of nativity.

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## SUPPLEMENTARY MATERIAL

The following material is available to download from [www.blackwell-synergy.com/loi/ddi](http://www.blackwell-synergy.com/loi/ddi)

**Appendix S1** Field investigations were carried out from 3 April to 18 April 1999 in Yunnan, from 1 August to 10 September 2001 in Yunnan and Sichuan, from 28 August to 20 September 2002 in Guizhou, from 28 March to 7 May 2003 in Yunnan and Sichuan, from 2 to 25 November 2003 in Guangxi, and from 10 September to 2 October 2004 in Sichuan and Chongqing.