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Predicting potential distribution of chestnut phylloxerid (Hemiptera: Phylloxeridae) based on GARP and Maxent ecological niche models

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Keywords

Castanea crenata, *Castanea mollissima*, *Moritziella castaneivora*, genetic algorithm, potential distribution

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Abstract

The chestnut phylloxerid, *Moritziella castaneivora,* has been recently recorded as a forest pest in China. It heavily damaged chestnut trees and has caused serious economic losses in some main chestnut production areas. In order to effectively monitor and manage this pest, it is necessary to investigate its potential geographical distribution worldwide. In this study, we used two ecological niche models, Genetic Algorithm for Rule-set Production (GARP) and Maximum Entropy (Maxent), along with the geographical distribution of the host plants, Japanese chestnut (*Castanea crenata*) and Chinese chestnut (*Castanea mollissima*), to predict the potential geographical distribution of *M. castaneivora*. The results suggested that the suitable distribution areas based on GARP were general consistent with those based on Maxent, but GARP predicted distribution areas that extended more in size than did Maxent. The results also indicated that the suitable areas for chestnut phylloxerid infestations were mainly restricted to Northeast China (northern Liaoning), East China (southern Shandong, northern Jiangsu and western Anhui), North China (southern Hebei, Beijing and Tianjin), Central China (eastern Hubei and southern Henan), Japan (Kinki, Shikoku and Tohoku) and most parts of the Korean Peninsula. In addition, some provinces of central and western China were predicted to have low suitability or unsuitable areas (e.g. Xinjiang, Qinghai and Tibet). A jackknife test in Maxent showed that the average precipitation in July was the most important environmental variable affecting the distribution of this pest species. Consequently, the study suggests several reasonable regulations and management strategies for avoiding the introduction or invasion of this high-risk chestnut pest to these potentially suitable areas.

Introduction

The chestnut phylloxerid, *Moritziella castaneivora* Miyazaki, 1968 (Hemiptera: Phylloxeridae), is a newly recorded forest pest in China which mainly harms Japanese chestnut (*Castanea crenata*) and Chinese chestnut (*Castanea mollissima*) trees. In general, *M. castaneivora* infests flowers and fruits of *C. crenata* and *C. mollissima* and causes yellowed chestnuts, stunted growth and premature fruits drop (fig. 1). *Moritziella castaneivora* has already caused severe economic losses (Jiang et al. 2006; Zhang et al. 2007). At present, *M. castaneivora* has only been recorded in Japan (Takashi et al. 1972; Ôgane 1975; Sasakawa and Shiozawa 1979; Nakagaki and Yanagibashi 1990) and some provinces of China (e.g. Liaoning, Hebei, Shandong, Henan, Zhejiang and Jiangsu) (Zheng 2004; Cheng et al. 2005; Jiang et al. 2006;

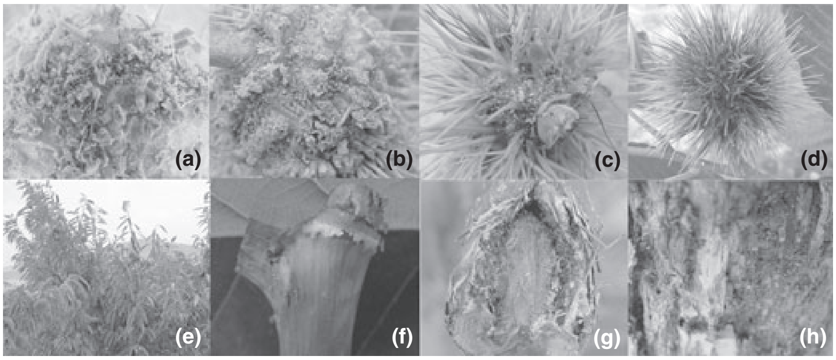

Fig. 1 Eggs, nymphs and adults of apterous oviparous females of *Moritziella castaneivora* and damage characteristics on *Castanea crenata*. (a–d) Damage to immature burs, (e) harm to the trees, (f–h) infestations in some shady gaps of branches and tree bark.

Zhang et al. 2007). *Castanea crenata* is mainly distributed in Japan, the Korean Peninsula and China, respectively, and *C. mollissima* is widely distributed in China. In recent years, *M. castaneivora* has also been found in some areas of China where Japanese chestnuts have been planted since 1960 (Liu et al. 2002). *Moritziella castaneivora* is considered an invasive species, introduced to China via seedling transportation from Japan or Korea (Zhang et al. 2007).

Moritziella castaneivora seriously threatens the quality and quantity of chestnuts *in China and Japan, which are the world's largest chestnut producers*. For example, in Japan, there were over 7000 ha of chestnut orchards in Ibaraki; more than 1000 ha were damaged and about 200 ha showed almost total crop failure, due to *M. castaneivora* (Nakagaki and Yanagibashi 1990). In China, *M. castaneivora* spread over 2700 ha in some orchards of the Shandong Province, and chestnut production was reduced by 30–40% (Zhang et al. 2007; Wang and Wang 2006). Due to overlapping generations, a high population growth rate and the lack of natural enemies, it is very difficult to control *M. castaneivora*. In addition, the geographical distribution of *M. castaneivora* depends on many factors, such as temperature, precipitation, altitude and vegetation respectively. Being a monophagous species, the most important factor influencing the distribution of *M. castaneivora* is regarded its host plants.

The geographical distribution of *M. castaneivora* in China is largely unknown, due to its small size (0.87–1.02 mm) and preference for shady locations (Jiang et al. 2006). It has a special holocyclic life cycle without active host transfer because of wingless morphs. In general, *M. castaneivora* has about 10 generations per year and asexual generations overlap (Zheng 2004; Cheng et al. 2005). Overwintering eggs are deposited under bark on tree trunks and in some shady gaps of branches. The fundatrices or stemmothers of *M. castaneivora* hatch during late April, and continue to breed on the primary host plants. When chestnut tree blossom starts, the second generation nymphs move and begin to damage flowers and buds. In July, the population size of *M. castaneivora* rapidly increases, and apterous oviparous females usually lay 30–80 eggs. *Moritziella castaneivora* usually has the highest population density from August to September, when thousands of individuals damage the chestnut burs and are able to complete one generation within only 1 week. From the middle of September to early October, the sexual generation of *M. castaneivora* mates to oviposit for overwintering (Cheng et al. 2005). The coming year's populations mainly originate from overwintering eggs under the bark on tree trunks and from some shady branch gaps.

In recent years, ecological niche modelling has been considered a useful tool to assess the potential geographical distribution of species, and has been applied to the fields of ecology, biogeography, evolution and conservation biology, among others (Ganeshaiah et al. 2003; Levine et al. 2004; Guisan and Thuiller 2005; Elith et al. 2006; Peterson et al. 2007). The Genetic Algorithm for Rule-set Production (GARP) has also been extensively used to model the potential geographical distribution of species in recent years and requires species distribution records and a set of environmental variables as inputs (Stockwell and Noble 1992; Li et al. 2005; Xue et al. 2005; Stockman et al. 2006; Zhou et al. 2007). The Maximum Entropy model (Maxent) is a new, general-purpose machine learning method which has many advantages making it well-suited for species distribution modelling. Maxent utilizes continuous and categorical data, incorporates interactions between different variables (Phillips et al. 2006), is good at avoiding commission errors (Pearson et al. 2007) and has a better performance than other ecological niche models in predicting the distribution of species, when only a limited number of sample localities are available (Elith et al. 2006; Hernandez et al. 2008). Both methods take into account temperature, precipitation, elevation and other variables, potentially influencing the distribution of species. Both methods also make use of known occurrences and pseudo-absence data re-sampled from the set of pixels where the species in question is not known to occur (Peterson et al. 2007; Wang et al. 2007). In addition, a recent comprehensive comparison of both presence-only modelling techniques indicates that Maxent and GARP have better predictive accuracy than other methods (Elith et al. 2006; Hernandez et al. 2006).

Here, we apply GARP and Maxent models to predict the potential distribution of *M. castaneivora*. The main aims of the study were to identify possible distribution areas of the species, estimate the risk of introduction of *M. castaneivora* to other parts of the world and gain some insights into the factors controlling the invasion.

Materials and Methods

Occurrence data

The occurrence locations of *M. castaneivora* were mainly based on our extensive field surveys in central and eastern China from May to October during 2007–2008. We also used some related references (Ôgane 1972, 1975; Sasakawa and Shiozawa 1979; Nakagaki and Yanagibashi 1990; Zheng 2004; Cheng et al. 2005; Jiang et al. 2006; Zhang et al. 2007). Occurrence records for both host plants, *C. crenata* and *C. mollissima* were mainly obtained from two databases, the Global Biodiversity Information Facility and the Chinese Virtual Herbarium databases. The longitude and latitude of occurrence locations were obtained by using the Geographic Names Database, and the geographical coordinates of collection localities were recorded using a Global Positioning System receive. Using the above sources, the distributional localities of *M. castaneivora* were compiled into a database.

For *C. crenata*, we obtained 21 distribution records in China and 235 records in Japan and on the Korean Peninsula, totalling 256 records in East Asia. Similarly, we obtained 229 distribution records of *C. mollissima* in China, including most Chinese areas except Qinghai, Xinjiang, Hainan, Inner Mongolia and Heilongjiang Province, respectively, and four records from Korea. The total number of distributional records for *C. crenata* was 233 in East Asia. The elevation range of the sample sites ranged from less than 100 m to more than 2400 m a.s.l. (fig. 2).

Following several surveys during 2007–2008, *M. castaneivora* was found in six provinces and two autonomous regions in China, including 22 counties: Liaoning (3), Shandong (9), Jiangsu (1), Hebei (5), Henan (1), Zhejiang (1), Beijing (1) and Tianjin (1) (table 1). At present, the most northern sample locality was in Kuandian County (40°72′N, 124°77′E), Liaoning Province; and the most southern sample locality was in Songyang County (28°45′N, 119°48′E),

Fig. 2 The distribution of *Castanea crenata* (blue triangles, 256 records), *Castanea mollissima* (green dots, 233 records) and *Moritziella castaneivora* (red crosses, 31 records).

Table 1 Occurrence points of *Moritziella castaneivora* based on field surveys and the literature

Locality	Longitude	Latitude	Host plants	Source
Lanshan District, Rizhao City, Shandong Province, China	119°13′E	35°04′N	*Castanea crenata* *Castanea mollissima*	Present study
Junan District, Linyi City, Shandong Province, China	118°83′E	35°17′N	*C. crenata*	Present study
Baoshan District, Jiaonan City, Shandong Province, China	119°97′E	35°88′N	*C. crenata*	Present study
Daliuhang District, Penglai City, Shandong Province, China	121°03′E	37°06′N	*C. mollissima*	Present study
Shantin District, Zaozhuang City, Shandong Province, China	117°47′E	35°10′N	*C. mollissima*	Present study
Licheng District, Jinan City, Shandong Province, China	116°92′E	36°32′N	*C. mollissima*	Present study
Daiyue District, Taian City, Shandong Province, China	117°13′E	36°18′N	*C. mollissima*	Present study
Feixian District, Linyi City, Shandong Province, China	117°97′E	35°25′N	*C. mollissima*	Present study
Tancheng District, Linyi City, Shandong Province, China	118°03′E	34°62′N	*C. mollissima*	Present study
Tongbai District, Xinyang City, Henan Province, China	113°40′E	32°35′N	*C. crenata* *C. Mollissima*	Present study
Miyun District, Beijing City, China	116°08′E	40°48′N	*C. mollissima*	Present study
Jixian District, Tianjin City, China	117°07′E	40°03′N	*C. mollissima*	Present study
Xinglong District, Chengde City, Hebei Province, China	117°05′E	40°40′N	*C. mollissima*	Present study
Sujiawa District, Zunhua City, Hebei Province, China	117°97′E	40°18′N	*C. mollissima*	Present study
Qianxi District, Tangshan City, Hebei Province, China	118°32′E	40°13′N	*C. mollissima*	Present study
Qinglong District,Qinhuangdao City, Hebei Province, China	118°93′E	40°40′N	*C. mollissima*	Present study
Jiangjunmu District, XingtaiCity, Hebei Province, China	114°02′E	37°22′N	*C. mollissima*	Present study
Songyang District, Lishui City, Zhejiang Province, China	119°48′E	28°45′N	*C. mollissima*	Present study
Fecheng District, Dandong City, Liaoning Province, China	124°03′E	40°47′N	*C. crenata*	Present study
Zhenxing District, Dandong City, Liaoning Province, China	124°37′E	40°13′N	*C. crenata*	Present study
Gulouzi District, Kuandian City, Liaoning Province, China	124°77′E	40°72′N	*C. crenata*	Present study
Chenlou District, Pizhou City, Liaoning Province, China	117°98′E	34°32′N	*C. crenata*	Present study
Tochigi-ken, Akakura, Japan	139°75′E	36°75′N	*C. crenata*	Ôgane (1972, 1975)
Oyama-shi, Tochigi, Japan	139°80′E	36°30′N	*C. crenata*	Ôgane (1972, 1975)
Gifu-ken, Japan	137°00′E	35°75′N	*C. crenata*	Ôgane (1975)
Nara-ken, Japan	136°00′E	34°50′N	*C. crenata*	Ôgane (1975)
Tottori-ken, Japan	134°00′E	34°00′N	*C. crenata*	Ôgane (1975)
Ibaragi-ken, Japan	135°55′E	34°85′N	*C. crenata*	Ôgane (1975)
Ishikawa- Ken, Japan	136°75′E	36°75′N	*C. crenata*	Ôgane (1975)
Ashikaga-shi, Tochigi, Japan	139°45′E	36°33′N	*C. crenata*	Nakagaki and Yanagibashi (1990)
Kyoto-fu, Japan	135°50′E	35°17′N	*C. crenata*	Ôgane (1972); Sasakawa and Shiozawa (1979); Nakagaki and Yanagibashi (1990)

These occurrence points are from field surveys, the related specimens of the species were deposited in the Zoological Museum of the Institute of Zoology, Chinese Academy of Sciences, Beijing.

Zhejiang Province. We also obtained nine Japanese distribution locations for this species (fig. 2).

GARP analysis

Genetic Algorithm for Rule-set Production (version 1.1.6) was used to predict the distribution of species (Stockwell and Noble 1992). We used 28 environmental data layers, including aspects of climate (temperature and precipitation) and topography (e.g. elevation, slope and aspect), potentially influencing the distribution of *M. castaneivora* at regional scales. Climate layers were obtained from the WorldClim dataset (Hijmans et al. 2005) and consisted of 25 variables expressing different limiting aspects of temperature and precipitation for this species. Three other topography data layers were obtained from the U.S. Geological Survey's Hydro-K data set (table 2).

The occurrence data of *M. castaneivora* was divided into two parts. We randomly selected 75% of the data for model training, and the remaining data (25%) were used for model testing. We used the bioclimatic variables as described above. Then, the GARP analyses were performed with the following optimization parameters: 250 runs, 0.01 convergence limit and up to 1000 maximum iterations. Four rule types (atomic, range, negated range and logistic regression) were employed and we assigned other parameters to default values. Finally, 'best subset' models and 'ARC/INFO Grids' were selected for output maps. The ten best models were summed in

Table 2 Environmental variables used in GARP and Maxent models

Variable code	Variable type	Data source
bio1	Annual mean temperature	WorldClim
bio2	Mean diurnal range: mean of monthly (max temp–min temp)	WorldClim
bio3	Isothermality: (P2/P7) × 100	WorldClim
bio4	Temperature seasonality (SD × 100)	WorldClim
bio5	Maximum temperature of warmest month	WorldClim
bio6	Minimum temperature of coldest month	WorldClim
bio7	Temperature annual range (P5–P6)	WorldClim
bio8	Mean temperature of wettest quarter	WorldClim
bio9	Mean temperature of driest quarter	WorldClim
bio10	Mean temperature of warmest quarter	WorldClim
bio11	Mean temperature of coldest quarter	WorldClim
bio12	Annual precipitation	WorldClim
bio13	Precipitation of wettest month	WorldClim
bio14	Precipitation of driest month	WorldClim
bio15	Precipitation seasonality (coefficient of variation)	WorldClim
bio16	Precipitation of wettest quarter	WorldClim
bio17	Precipitation of driest quarter	WorldClim
bio18	Precipitation of warmest quarter	WorldClim
bio19	Precipitation of coldest quarter	WorldClim
prec1	January average precipitation	WorldClim
pre7	July average precipitation	WorldClim
tmin1	January average minimum temperature	WorldClim
tmaxl	January average maximum temperature	WorldClim
tmax7	July average maximum temperature	WorldClim
tmin7	July average minimum temperature	WorldClim
dem	Elevation	USGS
slope	Slope	USGS
aspect 2	Aspect	USGS

ArcView GIS (version 3.2) (RSRI 1999) to produce a single final distribution map. Different map colours corresponded to different fitting indices in the potential distribution map. The analysis base map (China 1 : 4 000 000) was obtained from the National Fundamental Geographic Information System.

Maxent analysis

We used Maxent software (version 3.2.19) (Phillips et al. 2006), the same set of environmental variables and the same proportion of occurrence data for training and testing, as used in the GARP analyses. A set of four possibilities, such as logistic regression, bioclimatic rules, range rules and negated range rules were employed. The algorithm runs either 1000 iterations of these processes or until convergence. This model produced prediction values ranging from 0 to 100, representing cumulative probabilities of occurrence. Predictions were mapped in DIVA-GIS (version 5.2) (Sundar and Mitsuko 2005). A jackknife test was used to measure variable importance in model development, and receiver operating curve analysis (ROC) was used to assess model quality (Fielding and Bell 1997). A ROC plot was built by plotting the sensitivity values and the false positive fraction for all available probability thresholds (Manel et al. 2001). The area under the curve (AUC) was a measure of the area under the ROC, ranging from 0.5 to 1.0.

Results

Predicted potential geographical distribution

The results suggested that the suitable distribution areas based on GARP were general consistent with those resulting from Maxent, but the former prediction areas were more extensive than the latter's. Based on a comparison and analysis of the predictions from the two models, the most suitable areas were mainly restricted to Northeast China (northern Liaoning), East China (southern Shandong, northern Jiangsu and western Anhui), North China (southern Hebei, Beijing and Tianjin) and Central China (eastern Hubei and southern Henan). Secondly, some regions, such as some areas of Liaoning, Hebei, Henan, Anhui, Jiangsu, Hubei, Hunan, Sichuan, and

Chongqing, were suitable to the species, too. The remaining provinces or autonomous regions had low suitability or were unsuitable regions, namely, Xinjiang, Qinghai, Tibet, Yunnan, Guangdong, Guangxi, Hainan, Taiwan, Gansu, Inner Mongolia, Heilongjiang, Jilin, Shanxi, Ningxia and Guizhou, respectively. In addition, Japan (e.g. Kinki, Shikoku and Tohoku) and most parts of the Korean Peninsula were suitable regions (fig. 3).

Evaluation of models and the importance of environmental variables

A model with AUC values approaching 1.0 is usually considered a good model, while AUC values close to 0.5 are considered no better than random. In this study, the AUC value for the training data was 0.999 and the AUC value for the test data was 0.998, indicating a high level of accuracy for the Maxent

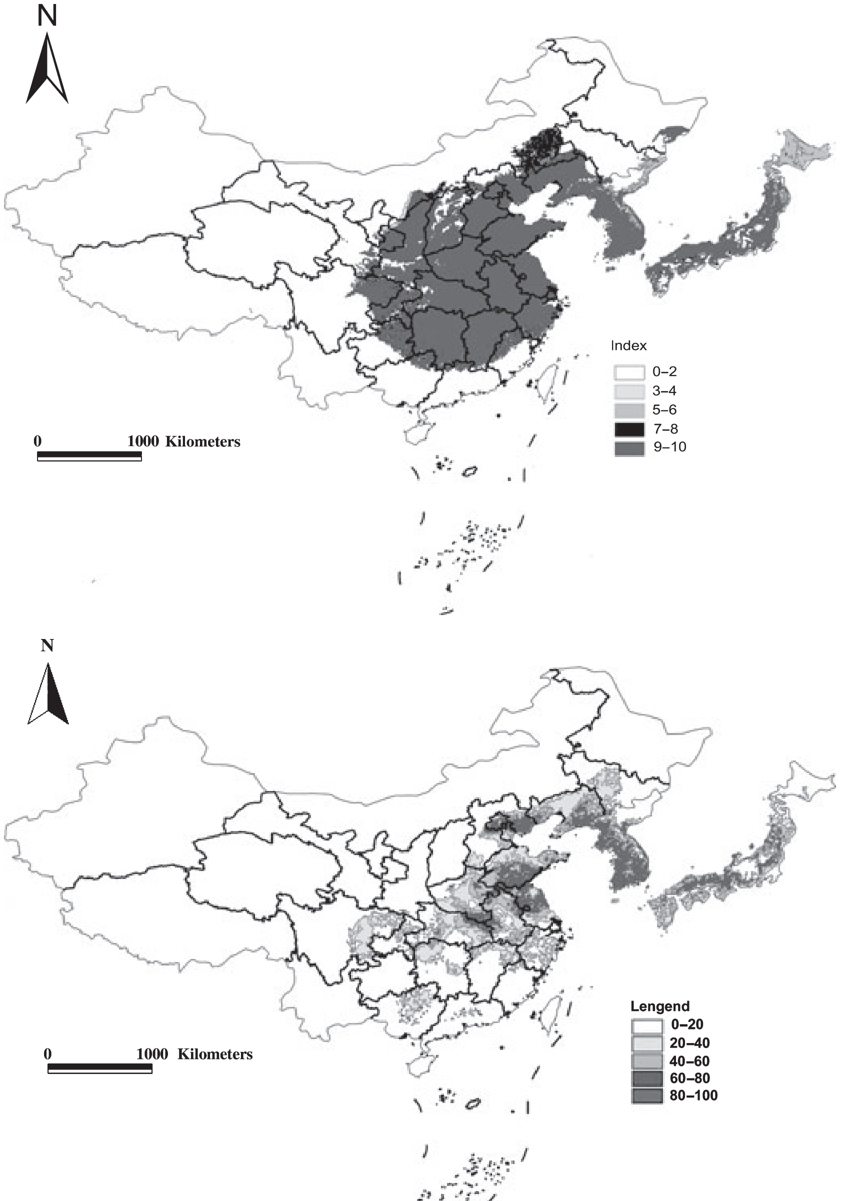

Fig. 3 The potential geographical distribution of *Moritziella castaneivora* using GARP (above) and Maxent (below). The red colour indicates areas with a high probability of occurrence for *M. castaneivora*, the blue and green represent moderately high probability of occurrence, the yellow colour represents low probability of occurrence and the white indicates areas not suitable for *M. castaneivora*.

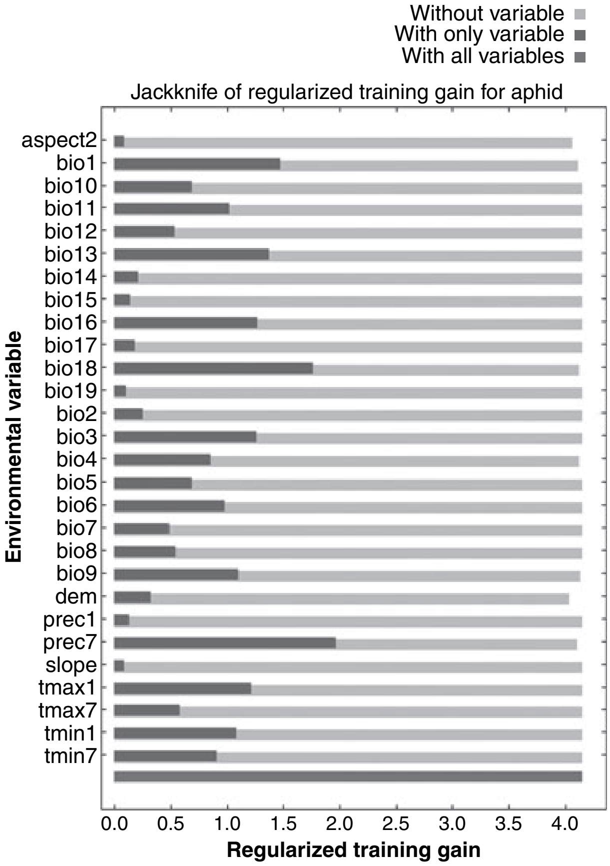

Fig. 4 Jackknife test of individual environmental variable importance (blue bars) in the development of the Maxent model relative to all environmental variables (red bar).

predictions (figures are not shown). These results suggest that Maxent had a high predictive power. In the Jackknife procedure, average precipitation in July had the highest gain when used in isolation (fig. 4). This indicated that the average precipitation in July was the most important environmental variable influencing the distribution of this species. In addition, some temperature and precipitation variables, such as annual mean temperature, January average minimum and maximum temperatures, mean temperatures of driest and coldest quarters, precipitation of wettest month, precipitation of wettest and warmest quarters may also influence this species' distribution to some extent (fig. 4).

Discussion

The results indicate that *M. castaneivora* will potentially be able to colonize seven provinces and two autonomous regions in China. In these regions, there are suitable climate conditions (11–17°C annual mean temperature, 500–1600 mm annual mean precipitation), and no climatic barriers to the introduction and cultivation of *C. mollissima*, which can grow in extremely cold temperatures (−30°C) with an annual mean temperature of 10–15°C, annual precipitation range from 500 to 1500 mm and altitudinal range from 50 to 2800 m (Feng et al. 2007). Based on the predicted distribution areas, Japan (e.g. Kinki, Shikoku and Tohoku) and most parts of the Korean Peninsula are the most suitable areas. It was obvious that *M. castaneivora* did not occur in some regions where *C. mollissima* and *C. crenata* were not cultivated, even if the suitable regions were predicted by GARP and Maxent ecological niche models, such as some parts of southern Shandong. Not all of the regions currently cultivating *C. mollissima* will be suitable for *M. castaneivora*, such as Sichuan, Yunnan and Guizhou provinces. Therefore, the results indicate that combining the distribution of cultivated hosts and other environmental factors can improve the accuracy of predicting the potential distribution of *M. castaneivora* in the future. This will help developing effective management strategies to prevent the spread of this pest across extensive cultivation areas.

Ecological niche models often only describe the fundamental niche of a species, rather than its realized niche. The fundamental niche consists of many conditions that allow for a species' long-term survival, whereas the realized niche is the subset of the fundamental niche that a species actually occupies. Therefore, the realized niche may be smaller than the fundamental niche. Many factors influencing the dimensions of the realized niche are often not taken into account when we predict the potential geographical distribution of species, such as biotic interactions (competitors, predators or parasites), geographical barriers and recent human activities (Guisan and Zimmermann 2000; Broennimann et al. 2007; Giovanelli et al. 2008). In this study, some factors were not considered, such as possible interspecific competition between *M. castaneivora* and *Lachnus tropicalis* (van der Goot), the influence of predation by natural enemies, such as *Propylaea japanica* (Thunb.), *Chilocorus kuwanae* Silv. and *Coccinella septempanctata* L. respectively. Besides, in the past few decades many chestnut trees were cut down because of a decline in chestnut quality and quantities produced. This may have resulted in habitat loss of chestnut trees, thus the occurrence of *M. castaneivora* was no longer possible in these locations.

In general, several restrictions should be considered when using ecological niche models to predict the potential geographical distribution of a species, such as the choice of environmental data sets (Peterson and Cohoon 1999; Stockwell and Peterson 2002; Phillips et al. 2006). The month's environment data sets have a better predictive performance than that of annual averages (Stockwell et al. 2006; Wang et al. 2007). Therefore, taking into account the short life cycle of *M. castaneivora*, we selected monthly climate variables in the GARP and Maxent models. In addition, through a jackknifing procedure, the influence of each environmental variable on the model predictive ability could be assessed. Our results showed that July average precipitation strongly influenced predictions for *M. castaneivora*, while other temperature variables (e.g. annual mean temperature, minimum temperature of coldest month, mean temperature of driest quarter, mean temperature of coldest quarter, January average minimum temperature, January average maximum temperature) and precipitation variables (e.g. precipitation of wettest month, precipitation of wettest quarter and precipitation of warmest quarter) also influenced predictions for *M. castaneivora* to different degrees. Besides the effects of scale and resolution (Thuiller et al. 2004), the sampling intensity and methods, the choice of thresholds should also be considered (Liu et al. 2005).

The choice of predictive models should also be based on the quantity and quality of the occurrence data. Recently, several comparative analyses have investigated the efficacy of different methods for modelling species' distributions. Maxent has many advantages as compared to other ecological niche models in predicting the potential distribution of species. Specifically, it is possible to run models with small numbers of sample localities in Maxent (Elith et al. 2006; Hernandez et al. 2008). Our data indicated that the suitable distribution areas based on GARP were similar to those from Maxent; however, the former prediction areas were wider than the latter's except the overlap areas, and the results were consistent with the viewpoint of Hernandez et al. (2006). Stockwell and Peterson (2002) thought the number of occurrence localities may be too low to estimate the parameters of the model reliably. Therefore, we ought to add distribution records so that we can obtain more reliable prediction results. On the other hand, it is important to make use of the knowledge of a species' natural history, and patterns of habitat use to examine the prediction results by GARP and Maxent. A current land cover classification derived from remotely sensed data can be used to exclude highly altered habitats by humans (Anderson and Martínez-Meyer 2004).

In light of the high degree of harm to chestnuts, the high risk of spread and potential wide distribution of *M. castaneivora*, it is necessary to monitor and manage this pest immediately by appropriate measures and avoid dispersing it to other main chestnuts production areas. Although this pest has a low dispersive capacity, seedling transportation is one of the main mechanisms of its spread. Therefore, quarantine measures should be strictly applied when *C. crenata* and *C. mollissima* are introduced from Japan and Korea, or some areas of China where *M. castaneivora* is known to occur. In addition, a general investigation of the distribution of *M. castaneivora* should be conducted, especially in the occurrence locations and the potential geographical distribution areas of *M. castaneivora*. In order to control *M. castaneivora* effectively, we should investigate its biological characteristics and ecology. We can also use molecular methods to determine levels of genetic diversity, population genetic structure and phylogeography, which will contribute to the elucidation of the population structure and history of this pest. All these above efforts will help to determine appropriate management strategies, and eliminate or reduce its negative impact on chestnut production to a certain degree.

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