Using ecological niche modelling to predict geographical expansion of an invasive species *Bursaphelenchus xylophilus* in Asia

You-Hua Chen

College of Life Sciences, Wuhan University, P.R. China, 430072; e-mail: haydi@126.com

Summary. The potential distribution of *Bursaphelenchus xylophilus* in Asia was investigated through ecological niche modelling. The modelling procedure was developed based on night environmental variables. Principal component analysis was used to describe environmental niche differentiation of the species. The analysis identified temperature and precipitation as the most important factors affecting the invasiveness of *B. xylophilus*. This implied that water and energy played the dominant role in the potential spreading of *B. xylophilus*. No significant relationship was found between human population density and environmental niches exhibited by *B. xylophilus*. Further monitoring effect should be enhanced in those natural landscapes with moderate temperature and precipitation, for example, temperate zone in China, Japan and Korea. Areas with relatively low precipitation would suffer higher risk of the species as indicated by ecological niche visualization. Some areas in SW China will become highly susceptible to the species in the 2050 because of climate change. Controlling pest species *Monochamus alternatus* was a highly efficient surrogate for controlling *B. xylophilus* in the fieldwork. My findings contribute to further understanding the invasive ecology of *B. xylophilus* and have implications in sustainable integrated pest management practices.

Key words: *Bursaphelenchus xylophilus*, ecological niche modeling, GARP model, human population density, invasive species, principal component analysis.

Biological invasion induced by alien species is one of the most urgent global issues affecting humans (Zhu *et al.,* 2007). Increasing global trade and travel has increased the risks of introducing exotic species to new areas around the world (Xiong *et al.,* 2007). Nematode species is an important component contributing to global alien species. The invasive nematode *Bursaphelenchus xylophilus* is a destructive species in the forest industry because it causes serious damage to the trees in the genus *Pinus*. Generally this species has been regarded as the 'cancer' of pines in East Asia (Wang *et al.,* 2007).

Bursaphelenchus xylophilus presumably originated from North America and was transported to the southern Japanese island of Kyushu at the beginning of the 20th century (EPPO, 2007 and references therein). From Japan, *B. xylophilus* has spread to other East Asian countries - China and Korea (Liu *et al.,* 2003; Song & Xu, 2006). Native American conifers are mostly resistant to the species, while Asian species are susceptible (Han *et al.,* 2007; EPPO, 2007). This developmental dif-ferentiation leads to massive destruction of Asian pines.

Bursaphelenchus xylophilus is found mainly on *Pinus* spp. For example, *P. bungeana, P. densiflora, P. luchuensis, P. massoniana* and *P. thunbergii* (native in Asia) are the major plants attacked by the species (Song & Xu, 2006; EPPO, 2007). *Bursaphelenchus xylophilus* has two modes of life cycle, a propagative mode and a dispersal mode (Wingfield, 1983). In both cases, the nematodes are transmitted from one host to another by insects from the genus *Monochamus*, principally *M. alternatus* (Song & Xu 2006; EPPO, 2007).

Extensive amount of information exist on the use of ecological niche models to predict species' potential distribution (e.g. Xiong *et al.,* 2007; Zhu *et al.,* 2007). However, few studies have attempted to predict the geographical distribution of destructive nematodes (Boag *et al.* 1992; Neilson & Boag, 1996). In searching the historical literature, only the potential distribution of *Longidorus elongatus* and *Xiphinema diversicaudatum* were predicted (Boag *et al.,* 1991; Neilson & Boag, 1996; Boag *et al.,* 1997). But these previous studies on nematode

species' distribution are based on the CLIMEX or simple statistical model and only focused on the geographic region in Europe (e.g., Boag *et al.*, 1991, 1997). However, in recent years, major distribution modelling techniques have been developed and applied. Therefore, using new tools to identify high-risk hotspots for *B. xylophilus* will be an interesting research topic. In addition, predicting nematode species in Asian countries will provide a complementary perspective of global nematode distribution. In this study, new mathematical models were introduced to predict the geographic expansion of an invasive nematode species *B. xylophilus* in Asia.

Human population density is regarded as an important factor affecting species richness (Diniz *et al.*, 2006, 2007; Luck, 2007) and population structure (Telles *et al.*, 2007), both of which have great implications in conservation biogeography (Diniz *et al.*, 2006, 2007; Araujo & Rahbek, 2007). However, previous studies related only to native species, and it is not known whether there is any correlation between human population density and invasive species. It is hypothesized that human population density is not only correlated with invasive species richness (Luck, 2007), but also with the predicted suitable environmental niches of invasive species. We will test the latter assumption herein because the niche visualization is possible.

In summary, this study is principally to analyze the spatial patterns of *B. xylophilus* in Asia through ecological niche modelling. We will address the following ecological parameters for *B. xylophilus*: 1) potential distribution trend under the current climatic scenario; 2) potential distribution shift under a future climatic scenario; 3) visual description of predicted suitable niches and identification of important factors shaping the niches along environmental gradients; and 4) testing of possible relationship between human population density and ecological niches of the species.

MATERIAL AND METHODS

Distributional dataset. Due to the limitation of data collection, the geographical distributional records of *B. xylophilus* were only gathered in China between year 2000 and 2007. The data were collected through cumulative online and literature search. The final dataset is composed of 72 distribution records in China and is available upon request.

Environmental dataset. We used night environmental variables to develop prediction models,

which were all downloaded from the homepage of DesktopGARP software (http://www.nhm.ku.edu/desktopgarp/index.html). These include elevation, slope, aspect, annual average precipitation, radiation, annual average temperature, evaporation, annual average number of frost days and humidity. Additional predicted climatic data were downloaded from the data distribution centre of IPCC (http://www.ipcc-data.org/). Predicted results of the HadCM2 model, developed at the Hadley Centre, Bracknell, UK were chosen as the basal data for climatic change scenario (Peterson *et al.*, 2002; Jones *et al.*, 2003). HadCM2 has a spatial resolution of $2.5° \times 3.75°$ (latitude by longitude), and the representation produces a grid box resolution of $96° \times 73°$ grid cells (http://www.ipcc-data.org/is92/ hadcm2_info. html).

The data of worldwide human population density was downloaded from Gridded Population of the World Version 3 (GPW v3.0) (Center for International Earth Science Information Network, Columbia University; http://sedac.ciesin. columbia.edu/gpw).

Methods. The GARP method, the abbreviation of the full name 'Genetic Algorithm for Rule-set Production', was used as the ecological niche model to predict the potential distribution. As one of genetic algorithms, GARP model works in an iterative manner for rule construction, evaluation and incorporation or rejection to produce a heterogeneous rule-set describing the species' ecological niche (Stockwell & Peters, 1999; Peterson & Vieglais, 2001; Zhu *et al.*, 2007). As a genetic algorithm, GARP model has been applied widely in modelling species potential distribution (Peterson & Vieglais, 2001; Peterson, 2005; Ron, 2005; Li *et al.*, 2006; Zhu *et al.*, 2007). Herein we briefly introduce the genetic algorithms, which develop rules to build niche models by a process analogous to natural selection. First, the performance of sets of rules is evaluated. Only the rules with the highest performance are maintained for the next generation. Then, processes analogous to genetic mutation, recombination, and crossing over modify the rules randomly. Finally, the modified rules are selected before the next generation based on their performance. The process is iterated until additional generations do not improve the performance of the set of rules (Stockwell & Peters, 1999; Ron, 2005).

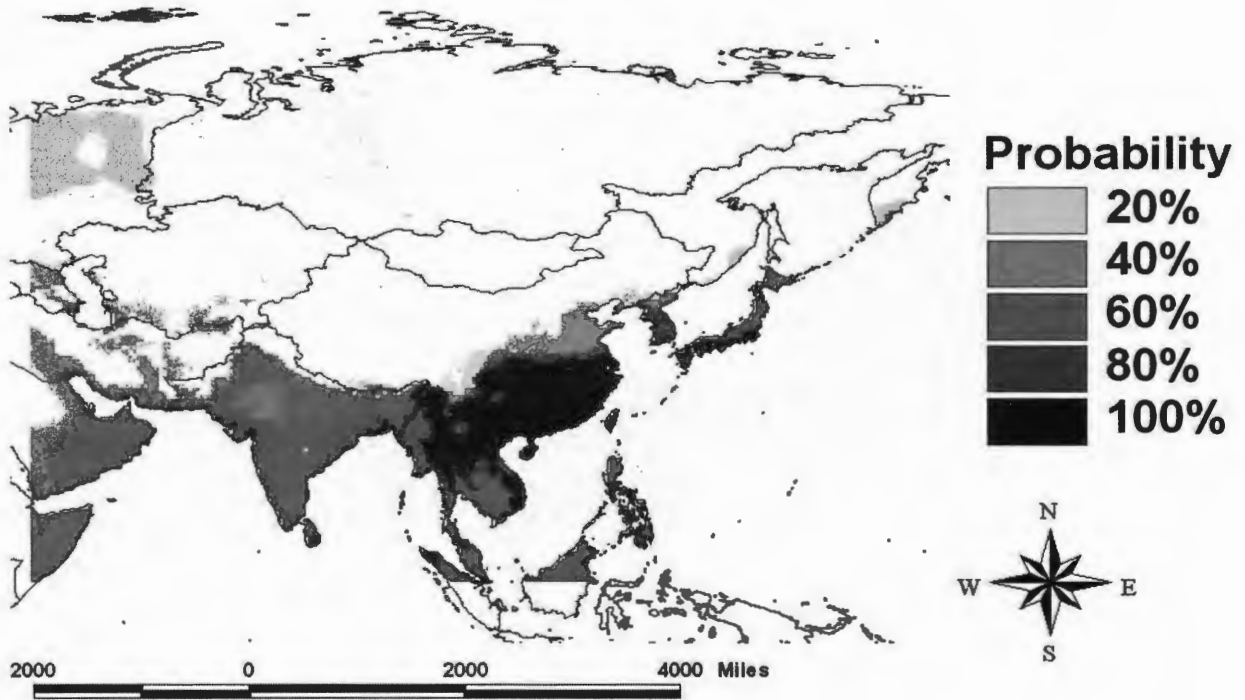GARP prediction modelling was developed using the free open source software OpenModeller

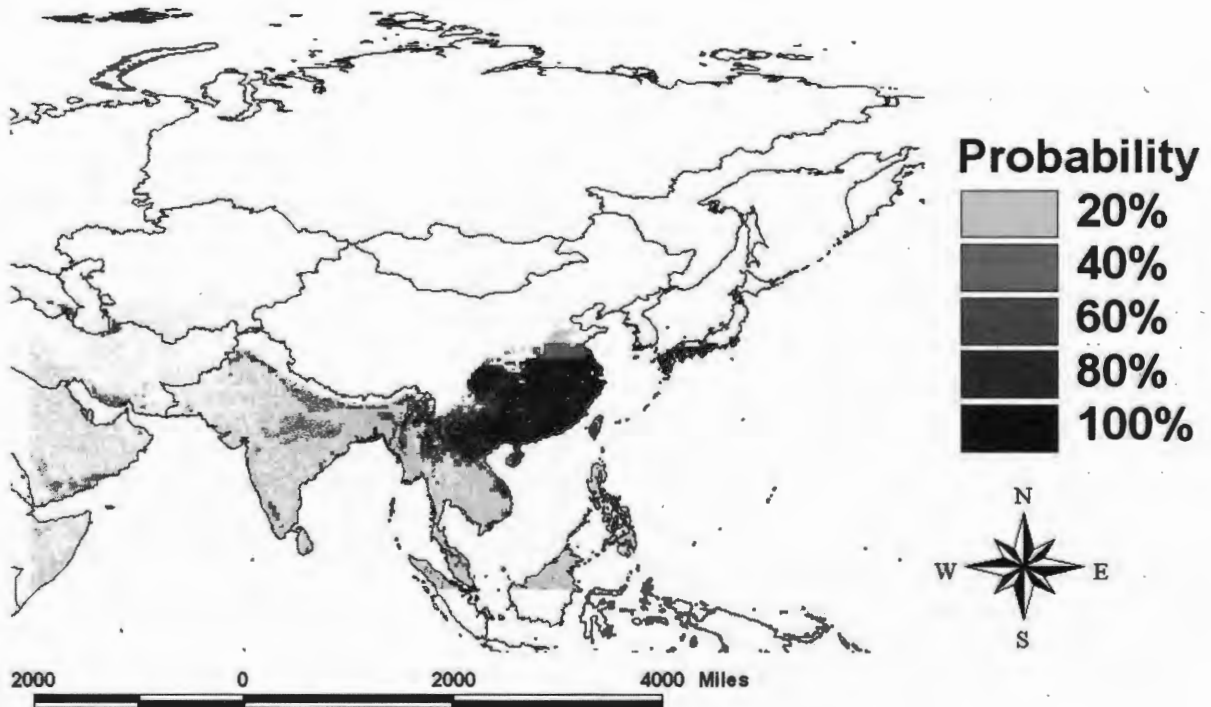**Fig. 1.** Current distribution range of *B. xylophilus* in Asia.

Fig. 2. Potential distribution range of *B. xylophilus* in Asia (year 2050).
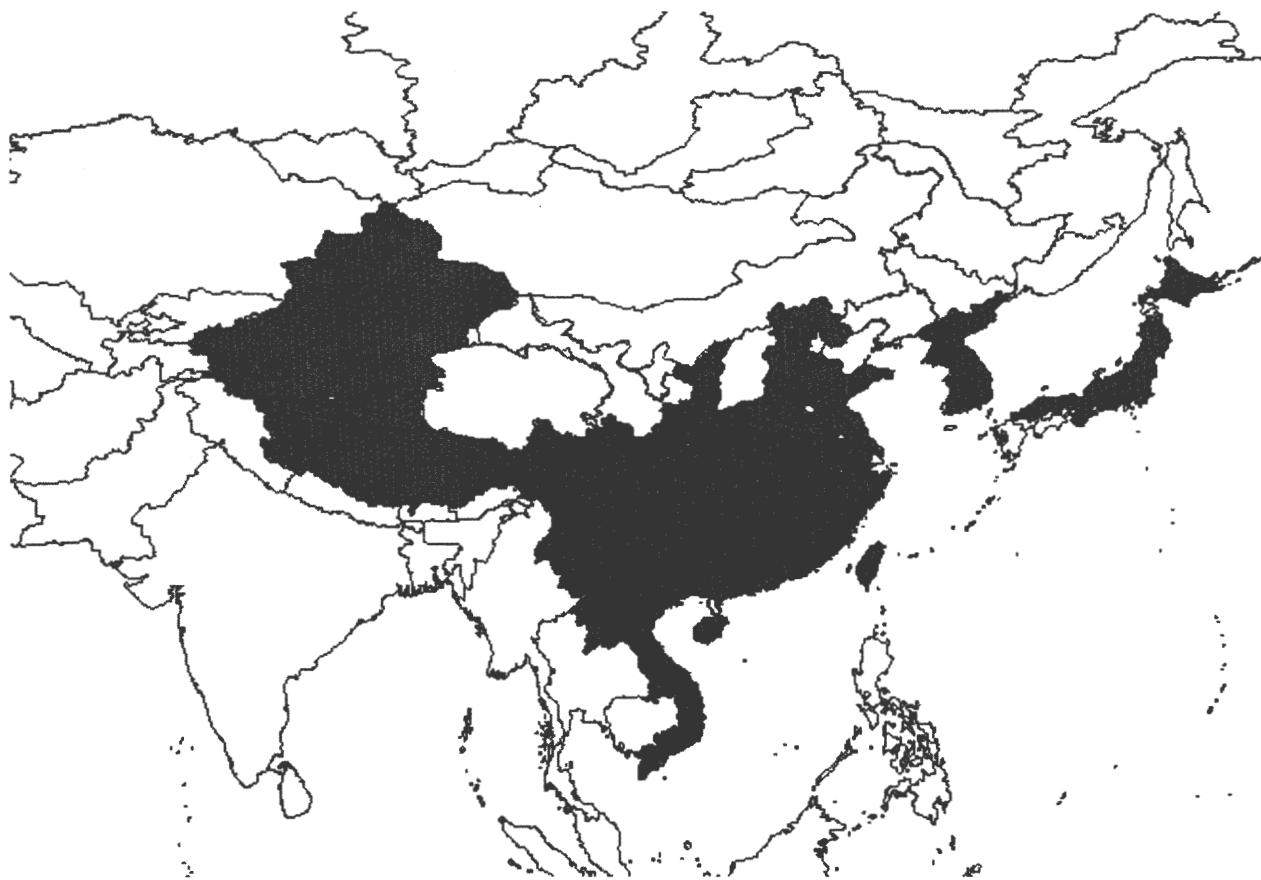
Fig. 3. The distribution range of the vector beetle *Monochamus alternatus* in Asia.

desktop version 1.0.5 (Sutton *et al.,* 2007), which was downloaded from http://openmodeller.source-forge.net/. OpenModeller was originally developed under the GPL License, based on several algorithms that were derived from ecological niches of species evaluating correlations between distributional occurrences and environmental characteristics, such as GARP, Bioclim, and Climate Space Model. We utilized the GARP algorithm with best subsets. The GARP model is projected onto geographic maps, and ArcView v3.3 (ESRI: http://www.esri.com/) is used to display the potential distribution expanding areas.

In the two-dimensional visualization of suitable niches for *B. xylophilus* (Peterson & Williams, 2008), for each environmental attribute, a *t*-test for two independent samples was applied to detect whether there was significant difference between the observed outbreak locations and predicted suitable sites.

Environmental data extracted from the predicted suitable range were analyzed by principal component analysis (PCA), with the aim of presenting suitable niche characteristic visually (Ron, 2005). PCA is implemented by the program MVSP v3.1i (Kovach Computing Services; http://www.kovcomp.com/) to order the invasion probabilities and spreading dynamics of *B. xylophilus* along the environmental gradients (Zhu *et al.,* 2007).

To infer whether there is a relationship between predicted suitable niches of invasive species and human population density, we carried out a simple regression analysis to fit the possible relationship using Statistica v6.0 (StatSoft, http://www.statsoft.com/).

RESULTS

Under current climatic scenario, we found that areas along the southern side of Yangtze River (Fig. 1) were the most potential outbreak sites for this nematode species. The southernmost boundary could reach countries of Indochinese Peninsula, such as Vietnam, Laos and Thailand.
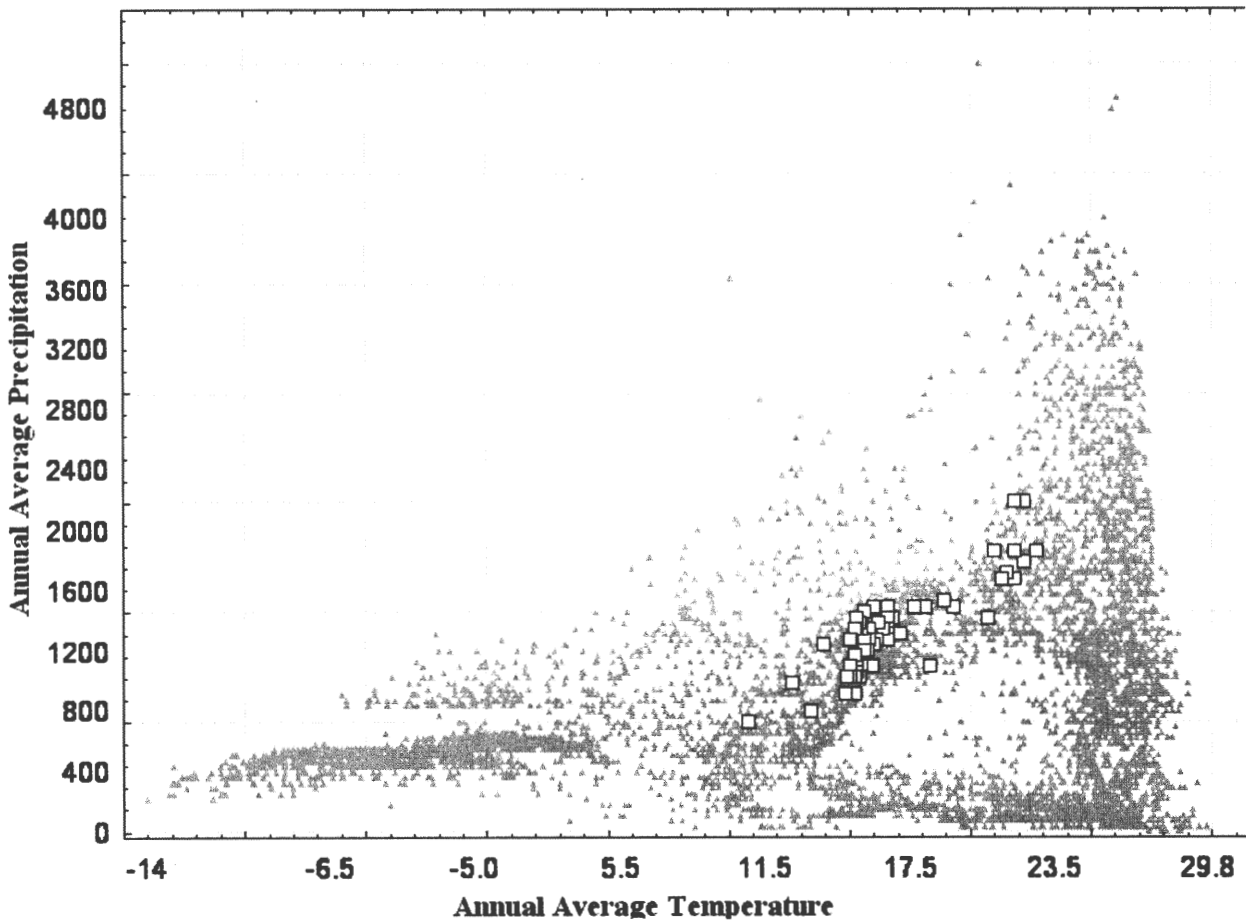
Fig. 4. Ecological niches of *B. xylophilus* in the suitable 2D environmental space produced by principal components I and II. Hollow squares indicate known localities; gray triangles indicated the 145063 predicted suitable locations.

Under future climatic scenario (in 2050 year), it was predicted that the geographical expansion of *B. xylophilus* would shift to southern areas of China (Fig. 2). The analysis further revealed that the suitable range will not cover the Shandong Peninsula, Liaodong Peninsula, North Korea, and Indochinese Peninsula in the predicted map. However, Sichuan Basin and Yunnan-Guizhou Plateau will become highly susceptible to this nematode.

To examine the accuracy of the distribution expansion range, the distribution of the host *M. alternatus* was mapped (Fig. 3) based on the summary from Song & Xu (2006). Results from this prediction demonstrated that areas with 100% probability of *B. xylophilus* occurrence fell within the known range of *M. alternatus*.

Three principal components with eigenvalues >1.5 accounted for 63.5% of the total variance based on the 9 variables that were measured (Table 1). Principal component I (axis I) was positively correlated with temperature (correlation: 0.493); while

principal components II and III were both positively correlated with precipitation (the correlations for axes II and III were 0.508 and 0.465, respectively).

Suitable niches (predicted probabilities $\geq$ 20%) for the first two essential environmental determinants were exhibited for comparing with those known outbreak localities (Fig. 4). The annual average temperature range for known localities is between 11.5°C and 23.5°C. None of 72 known localities is located in regions where annual average precipitation is below 800 mm. These known localities were arranged (Fig. 4) within the boundaries of predicted suitable niches defined by the bivariate environmental space of annual average temperature and annual average precipitation. Annual average temperature at known localities (Mean=16.49; SD=2.49) is not significantly different from the average at predicted localities (Mean=18.2; SD=9.15; T-test: p=0.1136). However, annual average temperature at known.
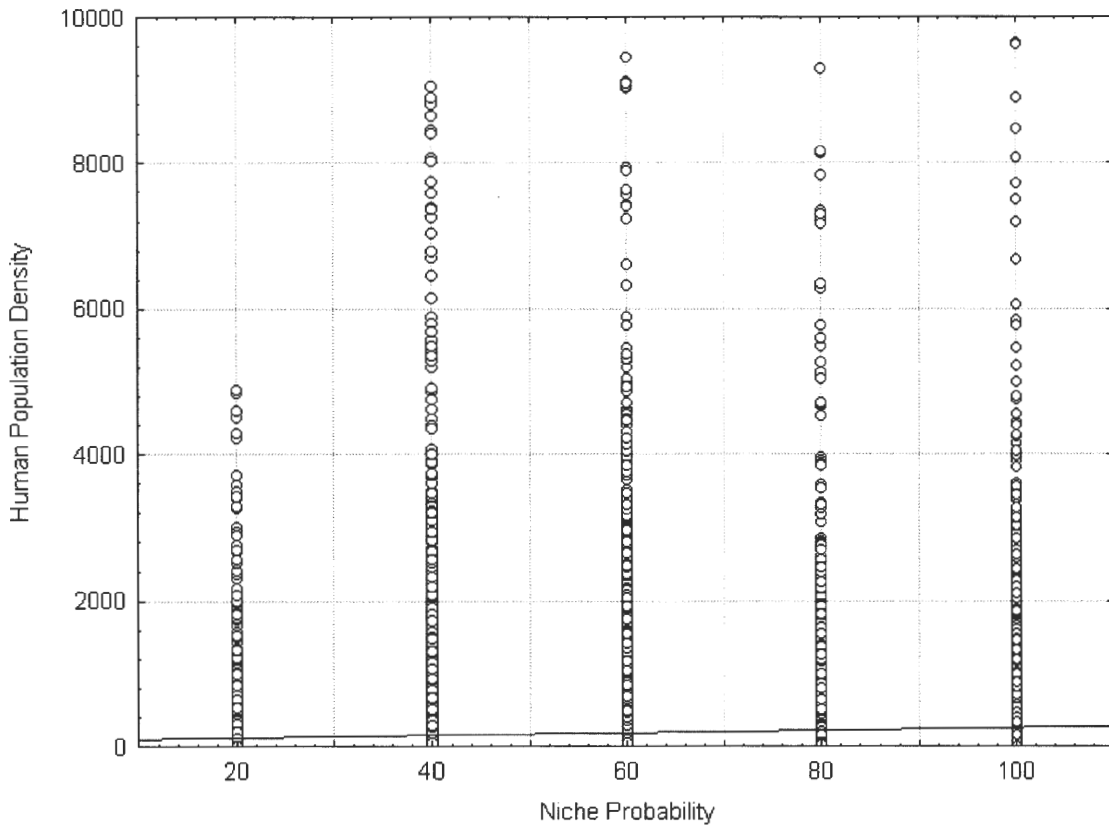
Fig. 5. The relationship between niche probability and human population density for *B. xylophilus* in Asia (The line denotes the simple regression fit: $R^2=0.007$; $p<0.0001$).

localities (Mean=1425.01; SD=317.41) and the average of predicted localities (Mean=1051.25; SD= 842.48) is significantly different from each other (T-test: $p<0.0001$). These results indicated that the species is expected to occur under a wide variety of temperature ranges (Ron, 2005), but has the distributional trend to invade arid areas with lower precipitation

There were no remarkable relationship between human population density and invasive suitable niches (Fig. 5). The linear fit is very ·low ($R^2=0.007$; $p<0.0001$). An analogous result is also obtained in polynomial regression analysis (not showed herein). The hypothesis that the predicted suitable environmental niche of *B. xylophilus* is correlated to human population density may be rejected.

DISCUSSION

The phylum Nematoda comprises some important pests of forest and agricultural products (Liu *et al.,* 2003; EPPO, 2007; Han *et al.,* 2007). Some nematode species, such as Tylenchida *spp.* and *Meloidogyne spp.*, can cause severe plant diseases. To understand more fully the epidemic character-istic of nematode species, it is important to reveal their ecological requirements on a spatial scale. In this study, applying ecological niche modelling, we made attempts to elucidate the distribution patterns of the nematode species *B. xylophilus*.

There are many proposed approaches for inferring species potential distribution, among which GARP model is the most robust and the most widely used (Peterson & Vieglais, 2001; Peterson, 2005). Because the maps generated from GARP could not be explained directly, principal component analysis was applied to reveal the underlying association between environmental factors and *B. xylophilus*. This kind of analysis has previously been used to reveal the distribution pattern of pathogens (Ron, 2005).

Environmental envelop analysis provides visual graphical display of fundamental niche characteristic of *B. xylophilus* influenced by concrete and tangible ecological parameters (Ron, 2005; Zhu *et al.,* 2007). Through principal component analysis, the pivotal variables shaping geographic distribution of invasive species (Table 1 & Fig. 4) could be obtained, the top ones of which are temperature and precipitation. Therefore, we could conclude that

water and energy are both vital to enhance the invasive success of *B. xylophilus* in pine trees. In general, moderate climatic parameters in the temperate zone of East Asia provide highly preferential condition for the invasiveness of *B. xylophilus*.

Table 1. Character loading of percentage of variance explained by the first three principal components (PC) for 9 environmental variables at 145063 predicted suitable locations in Asia (Fig. 4). * depicts the three most important variables correlated with each axis. The Abbreviations: ASP: aspects; FRS: annual average frost days; PRE: annual average precipitation; RAD: radiation; SLO: slope; TMA: annual average temperature; VAP: evaporation; WET: humidity; ELE: elevation.

	PC I	PC II	PC III
Eigenvalues	3.907	1.982	1.729
Percentage of variance explained (%)	32.559	16.516	14.409
ASP	-0.022	0.058	-0.045
FRS	-0.467*	-0.188	-0.049
PRE	0.01	0.508*	0.465*
RAD	0.441*	-0.055	-0.32*
SLO	-0.127	0.47*	-0.284
TMA	0.493*	0.128	0.012
VAP	0.09	-0.464*	0.302
WET	0.4	0.262	0.3
ELE	-0.37	0.252	0.396*

The geographic coincidence between the predicted range of *B. xylophilus* and the known occurrence of the host pest *M. alternatus* (Fig. 3) indicated that *M. alternatus* is a highly efficient surrogate for controlling *B. xylophilus* in the field. Although there are other hosts for *B. xylophilus*, *M. alternatus* was the preferred one for the propagation of the nematode (Wang *et al.,* 2007), Therefore, in practice, we suggested that the areas having populations of *Monochamus* species, especially *M. alternatus*, would be the first to be considered for spread of *B. xylophilus*. We also suggested richness hotspots in SW China (Myers *et al.,* 2000) such as Yunnan and Sichuan Provinces (Chen & Bi, 2007) have higher probabilities of invasion by the species under climatic change (Fig. 2). This result has positive implication for setting up necessary monitoring measures in SW China in preventing invasion of *B. xylophilus* (Wang *et al.,* 2007).

There was no significant relationship between potential invasive niches of *B. xylophilus* and human population density. This implied that the dispersal of invasive species is rather complex. Human activity is a factor possibly influencing the

distributional range but may not play a dominant role. This result is different to those studies showing a positive relationship between native species and human population (Diniz *et al.,* 2006, 2007; Telles *et al.,* 2007). To some extent, this demonstrated that the spatiotemporal trend of *B. xylophilus* is human-independent. The suitable environmental niches of *B. xylophilus* distribute homogenously in regions with various human population densities. Climatic attributes are superior to human population density in interpreting the potential distribution of the species. Other factors such as host dispersal ability and tree richness maybe also contribute to its invasive success in Asia, although these have not been tested here.

Although we present the predicted map under a future climatic scenario, this map is just a coarse assessment of the species' suitability under future climatic conditions, and is less explanatory compared with that of the current climatic scenario. The main reason for this is that climatic change is just one of the aspects regulating the distribution dynamics of invasive species. Other aspects such as unknown scourges, natural enemies and biotic resistance may jointly contribute to the future distribution range. In practice, the current predicted distribution range has more meaning than future predicted range.

On technical aspect, there are two packages implementing GARP model: OpenModeller and DesktopGARP. The advantage of OpenModeller compared to DesktopGARP is to allow layers with different resolutions to work together directly without transformation. This becomes convenient because we do not need to input formalized environmental layers, which reduce the preparation time prior to develop the modelling.

Lack of some known localities due to collection limitations do not significantly influence the predicted accuracy of the model. As evidenced in Figs. 1 and 2, the predicted range could reach those areas occupied earlier by *B. xylophilus* but lacking distributional information, such as Korea and Japan. In addition, as described above, most of the predicted range of *B. xylophilus* with highest probability (100%) is covered fully by the distributional range of its host *M. alternatus*. Both demonstrate the robustness of the prediction model merely using limited known distribution points.

In conclusion, under climate change, the potential distribution of *B. xylophilus* will spread to more southern areas of China where a biodiversity hotspot (Myers *et al.,* 2000) is located. The potential range will be constrained to S China and adjacent countries in SE Asia when climatic condition

becomes hot. Water and energy rather than physiological factors (i.e. altitude, slope, and aspect) play dominant roles in regulating the distributional trend of *B. xylophilus* through environmental envelope analysis. Moderate temperature and precipitation conditions will accelerate the invasive rate of the species. No direct relationship is found between predicted niches of the species and human population density.

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Chen You-Hua. Использование моделирования экологических ниш для предсказания географической экспансии инвазивного вида *Bursaphelenchus xylophilus* в Азии.

Резюме. Потенциал распространения *Bursaphelenchus xylophilus* в Азии исследован с помощью моделирования экологических ниш. Девять переменных, отражающих условия окружающей среды, использовались для построения моделей. Проведенный анализ выявил значения температуры и уровня осадков как основные факторы, ограничивающие распространение *B. xylophilus*. Это показывает, что влажность и инсоляция играют основную роль в ограничении *B. xylophilus*. Не было обнаружено связи между плотностью населения и наличием экологических ниш, освоенных *B. xylophilus*. Необходим дальнейший мониторинг в естественных экосистемах умеренного климата в Китае, Японии и Корее для контроля распространения этих нематод. Метод визуализации экологических ниш показывает, что наибольшему риску подвержены регионы со сравнительно низким уровнем осадков. Некоторые районы Юго-Восточного Китая могут к 2050 году оказаться весьма уязвимыми для *B. xylophilus* из-за происходящих климатических изменений. Контроль переносчиков – усачей *Monochamus alternatus* – может оказаться весьма эффективным средством ограничения распространения *B. xylophilus* в полевых условиях. Выявленные закономерности важны для понимания экологии инвазивного вида *B. xylophilus* и имеют значение для планирования мер борьбы с этими вредителями.