ORIGINAL ARTICLE

Global potential distribution of an invasive species, the yellow crazy ant (*Anoplolepis gracilipes*) under climate change

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Abstract

Changes to the Earth's climate may affect the distribution of countless species. Understanding the potential distribution of known invasive species under an altered climate is vital to predicting impacts and developing management policy. The present study employs ecological niche modeling to construct the global potential distribution range of the yellow crazy ant (*Anoplolepis gracilipes*) using past, current and future climate scenarios. Three modeling algorithms, GARP, BioClim and Environmental Distance, were used in a comparative analysis. Output from the models suggest firstly that this insect originated from south Asia, expanded into Europe and then into Afrotropical regions, after which it formed its current distribution. Second, the invasive risk of *A. gracilipes* under future climatic change scenarios will become greater because of an extension of suitable environmental conditions in higher latitudes. Third, when compared to the GARP model, BioClim and Environmental Distance models were better at modeling a species' ancestral distribution. These findings are discussed in light of the predictive accuracy of these models.

Key words: *Anoplolepis gracilipes*, BioClim, ecological niche modeling, Environmental Distance, GARP.

INTRODUCTION

An understanding of the potential distribution of an invasive species aids in the prediction of impacts associated with, and usually caused by, that species (Kriticos *et al.* 2005). Control efforts imposed at an early stage of invasion are more likely to be successful than once an invasion has progressed. If abiotic factors that influence invasion success for an invasive ant species are identified, we can use these factors to predict where and when each species will be found, resulting in more informed management decisions.

The yellow crazy ant (*Anoplolepis gracilipes*) has received increasing attention in recent times (Haines & Haines 1978; Holway *et al.* 2002; Gerlach 2004; Feldhaar *et al.* 2006; Drescher *et al.* 2007). This has been due to the negative impacts of this species on native vertebrate and invertebrate populations resulting from yellow crazy ant colonization of new areas. For example, in addition to attacking hatchling birds and reptiles *A. gracilipes* preys upon adult small mammals, birds and reptiles (Hill *et al.* 2003; Gerlach 2004; Drescher *et al.* 2007). This insect is among the top 100 invasive species, as listed by the International Union for Conservation of Nature (Lowe *et al.* 2000).

Although its exact origin remains unknown (Wetterer 2005), the yellow crazy ant has caused serious problems in infected areas, and the speed with which it spreads is almost unrivaled. Currently, most studies on this species are focused on the autoecology or population structure

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(Gerlach 2004, Abbott 2005, 2006; Feldhaar *et al.* 2006; Drescher *et al.* 2007), and understanding its spatial distributional pattern (Wetterer 2005; Harris *et al.* 2005; Commonwealth of Australia 2006; Harris & Barker 2007); however, the trans-continental distribution trend has not been investigated as comprehensively (Wetterer 2005). The present study aims to develop an invasive model for the yellow crazy ant at a global scale in order to assess the potential impacts of climate change on the spatial pattern of this species.

Ecological niche modeling, in response to the need of predicting exotic species' distribution, has gained popularity in recent times and the application of this technique to ant species is growing (Harris *et al.* 2005; Morrison *et al.* 2005; Xue *et al.* 2005; Harris & Barker 2007; Ulrichs & Hopper 2007; Ward 2007). The known climatic requirements or tolerances of a species, once parameterized and used in modeling, are termed climate envelopes or ecological requirements (Berry *et al.* 2002). There are a suite of tools available to predict the potential distribution of species, with these tools varying in the mathematical technique and framework they employ. Exemplary products include BIOCLIM (Busby 1991), DOMAIN (Carpenter *et al.* 1993), CLIMEX (Sutherst *et al.* 1995), GARP (Stockwell & Peters 1999), and Environmental Distance (Sutton *et al.* 2007). This study will perform ecological niche modeling for the yellow crazy ant under different climate change scenarios and utilize BioClim, GARP and Environmental Distance models.

MATERIALS AND METHODS

Yellow crazy ant distribution data

Records of the current global distribution *A. gracilipes* were obtained from James Wetterer (personal communication 2006). Excluding those that do not have explicit geological coordinates, the remaining 818 geo-referenced occurrence records were used as the input data for prediction.

Modeling tools

Predicting the geographic distribution of this species was done using the open source software OpenModeller (Version 1.0.5, Sutton *et al.* 2007). OpenModeller was originally developed under the GPL License, based on several algorithms derived from ecological niches of species and from evaluating correlations between distributional occurrences and environmental characteristics. The software includes the following models: GARP, Bioclim, Climate Space Model, Environmental Distance, Distance to

Average, and Minimum Distance. I utilized three representative models: GARP, BioClim and Environmental Distance for combined modeling. The GARP model has been successfully applied in many studies and typically has two types, GARP with best subsets and GARP with single performance. The former was chosen and referred to simply as GARP throughout this paper. GARP is a genetic algorithm that creates ecological niche models for species. The models describe environmental conditions under which the species should be able to maintain populations (Sutton *et al.* 2007). BioClim is an environmental envelope algorithm that identifies locations that have environmental values that fall within the range of values measured from the occurrence dataset (Nix 1986, Busby 1991, Hernandez *et al.* 2006). It is well-known for its long-term and far-ranging application. The Environmental Distance model is a generic algorithm based on environmental dissimilarity metrics (Sutton *et al.* 2007). The reason for selecting these three models was that some algorithms in OpenModeller are similar. For example, Environmental Distance, Distance to Average and Minimum Distance models are similar because they are based on distance measures. For brevity, I only selected Environmental Distance as the representative for this comparative analysis. All the models are projected onto geographic maps and the geographic information system software ArcView v3.3 (ESRI 2001) is used to display the potential distribution expanding areas.

Environmental data

OpenModeller offers flexibility in the selection of base environmental data layers. I used the following variables: the environmental layers provided by DesktopGARP, which include elevation, slope, aspect and climatic variables. Additional variables were also obtained online: the global vegetation layer was collected from National Geophysical Data Center (NGDG 2008). The layers global soil PH, soil moisture, soil organic carbon, potential vegetation, net primary productivity, growing degree days, average relative humidity, croplands percentage and potential evapotranspiration were obtained from Atlas of the Biosphere (2002). Although these 23 layers in all have different pixel sizes, they do not prematurely stop the implementation of OpenModeller. The algorithm GARP with best subsets in OpenModeller was used as the prediction procedure in this study.

The future environmental envelopes were derived from the predicted climate scenarios of the Intergovernmental Panel on Climate Change (IPCC). Most climate change studies use estimates of regional climate change from glo-
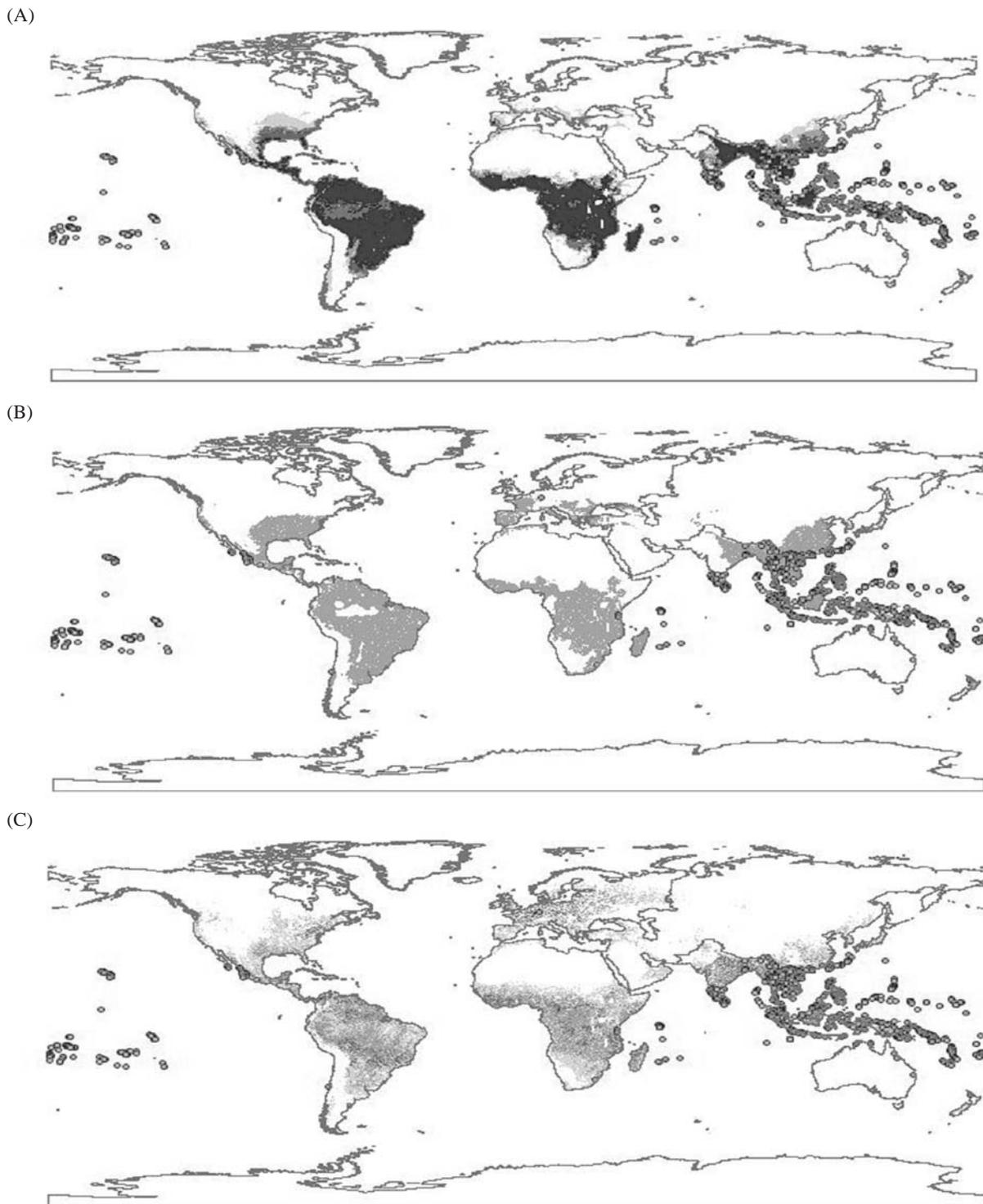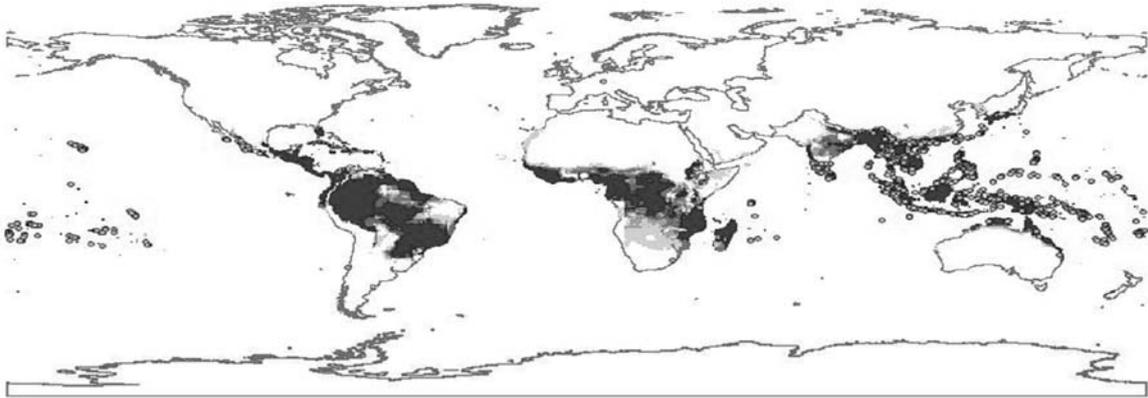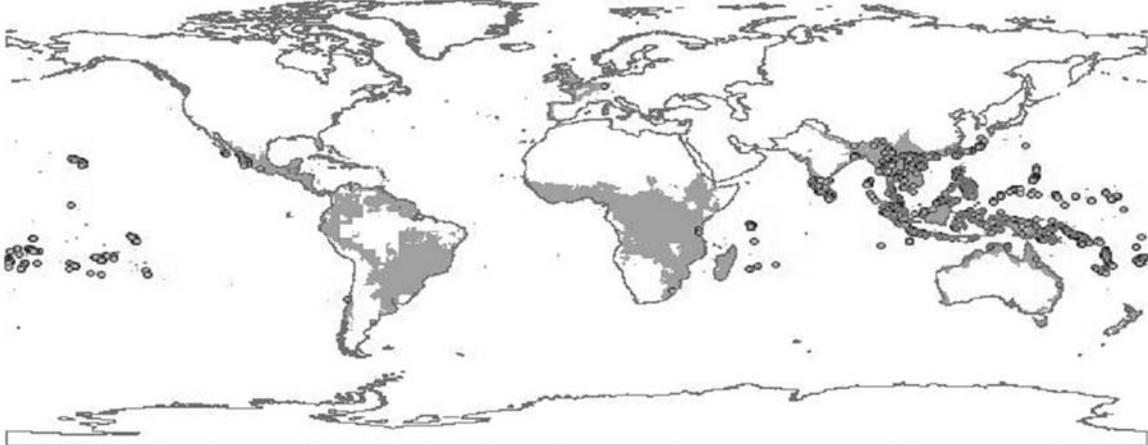
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Figure 1 Current potential distribution range of *A. gracilipes*. (A) GARP model; (B) BioClim model; (C) Environmental Distance model. Circle points indicate the observed occurrence of *A. gracilipes*. For individual model, the grey colors from light to heavy indicate the predicted probabilities from low to high.

(A)

(B)

(C)

Figure 2 Future potential distribution range of *A. gracilipes* (2050 year). (A) GARP model; (B) BioClim model; (C) Environmental Distance model. Circle points indicate the observed occurrence of *A. gracilipes*. For individual model, the grey colors from light to heavy indicate the predicted probabilities from low to high.
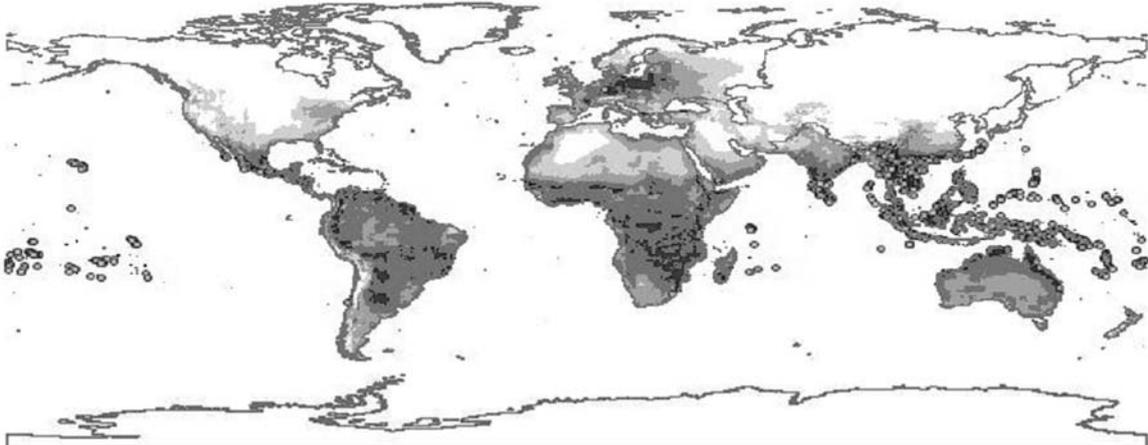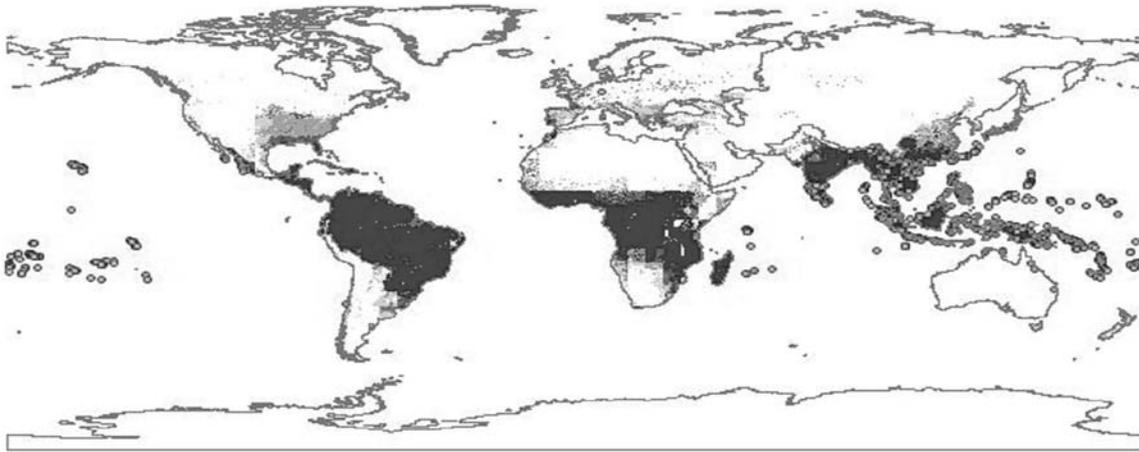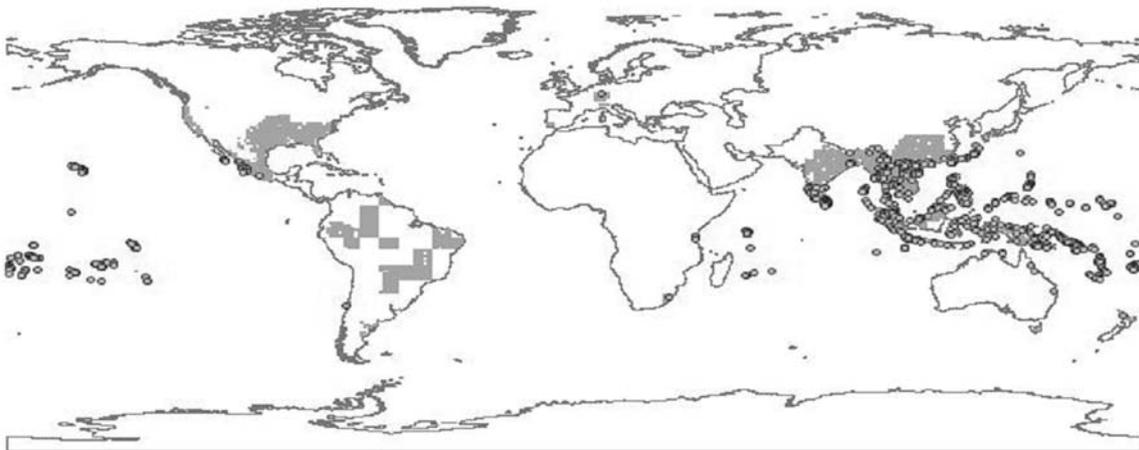
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Figure 3 Past potential distribution range of *A. gracilipes* (6000 yr B.P.) (A) GARP model; (B) BioClim model; (C) Environmental Distance model. Circle points indicate the observed occurrence of *A gracilipes*. For individual model, the grey colors from light to heavy indicate the predicted probabilities from low to high.

bal circulation models (GCMs), while the modeled data distributed by IPCC is regarded as one of the most recent GCM climate change scenarios recommended for climate change impact studies (Alexandrov *et al.* 2002). GCMs utilize physical equations and move heat, water vapor and momentum on a grid-box basis over the Earth's surface and at discrete levels in the atmospheric column. GCMs are also coupled to ocean models which move heat, momentum and salt within surface layers and at depth (Jones *et al.* 2003). The variables available from the IPCC included precipitation, evaporation, annual minimal temperature, annual maximal temperature, and annual average temperature. These factors, typically being the output of GCMs, represent the global surface climate characteristics over land areas.

The GCM used here is the second Hadley Centre coupled ocean-atmosphere integration (HadCM2). There are two experiment integrations in HadCM2, that is, HadCM2GG and HadCM2GS, and both predict the rise of global surface temperature between 3°C to 4°C by the year 2100. The experimental scenario I used herein is the HadCM2GS, which uses the combined forcing of all greenhouse gases as an equivalent CO_2 concentration and the negative forcing from sulfate aerosols. Compared to HadCM2GG (only using combined forcing of all greenhouse gases), HadCM2GS had a better fit to historic observation (Collison *et al.* 2000). Specifically, the resulting data for my modeling is the average output (HadCM2GSX) of the four members HadCM2GS1 to HadCM2GS4. HadCM2 has a spatial resolution of 2.5°×3.75° (latitude by longitude), and the representation produces a grid box resolution of 96×73 grid cells (please refer to the information homepage of HadCM2 model, John *et al.* 1997).

Past predicted climatic data were downloaded from the website of the Paleoclimate Modeling Intercomparison Project (Joussaume *et al.* 1999; PMIP 2005). I used the prediction model CCSR1 output data as the basal past predicted climatic data. The following environmental variables were used to substitute the same variables of the current environmental envelope to form the paleoclimatic data sets: evaporation, elevation, total precipitation and surface air temperature. The prediction time scenario is at about 6000 yr B.P. (years before present), corresponding to the period of the middle Holocene.

Model CCSR1 (Numaguti et al. 1995) is based on a simple global atmospheric model first developed at the University of Tokyo and further refined as the collaboration between Center for Climate System Research (CCSR) and the National Institute of Environmental Studies (NIES). It is intended for use as a community climate model. The

model is identical to the latest AMIP model (Gates 1992) except for different initial conditions and the Earth's orbital parameters. For PMIP, CCSR1 consists of runs 21, 6 and 0.

RESULTS

Current potential distribution

The worldwide potential range from the three models was consistent. Figures 1A, B, C show the current potential global range generated by the three models. The results showed that *A. gracilipes* has a relatively wide suitable range. The predicted distribution could cover a wide latitudinal range between 43 N and 46 S.

In Asia, a large area from the Yangtze River in China to tropical Asian latitudes (e.g. the Indian peninsula, Indo-China countries and the Malaysian peninsula) was predicted to be highly susceptible to invasion by this insect. In addition, most areas of the Korean peninsula and Japan were identified as having median affected risk.

In Africa, the highest risk from this insect occurred between 30 S and 15 N and was consistent among the three models. Most regions from tropical rainforest and subtropical monsoon climates were preferential areas for *A. gracilipes.* Nearly the entire Afro tropical region, except the south-western tip (Northern Cape Province of South Africa, and most areas of Namibia), was at high-risk in being infected by this insect.

In Australasia, suitable areas for this insect could reach to the north of New Zealand. In Europe, most areas of southern Europe including the Iberian Peninsula, France and Yugoslavia showed significant risk from crazy yellow ant invasion. Environmental Distance model (Fig. 1C) generated a greater number of suitable areas in Europe for this species compared to the other two models. In South America, most of the Amazonian tropical forest zones had a high probability of invasion from this insect, as does the southeastern area of North America.

Future potential distribution in 2050

Under a climatic scenario of the year 2050 (Figs. 2A, B, and C), the expansion of this insect would take place across Africa, Asia and Europe. Of note is that there were northward and southward shifts in the area of climatic preference for this ant, which was particularly evident in North America, Europe, South America and Australia. For example, in the map generated by the Environmental Distance model, North America, especially along coastal USA, has a high probability of invasion (Fig. 2C). Most areas in

South America, Europe and Australasia became susceptible under the Environmental Distance model (Fig. 2C). All three models had consistently predicted that Australia became a risk under climate a change scenario of 2050. BioClim and GARP models generated similar output maps, which indicated that the suitable range was decreasing (Figs. 2A, B). Nonetheless, Environmental Distance model seemed to overestimate future potential range because most arid areas in Africa and Australia were predicted suitable (Fig. 2C).

Past potential distribution

In ancestral distribution modeling, two of the three models, BioClim and Environmental Distance, generated similar results (Figs. 3B and C), while GARP overestimated the past potential range of *A. gracilipes* (Fig. 3A). The predicted range from GARP remained constant compared to the current modeled range. For BioClim and Environmental Distance models, the predicted range indicated that south Asia was highly suitable for *A. gracilipes* in the early Holocene compared to current areas of predicted suitability. In addition, partial regions from Europe, South America, and North America were shown to be at risk of invasion of this insect. Africa was found to have low occurrence probability for *A. gracilipes* in the two models and limited areas in Africa were found suitable (Figs. 3B and C).

DISCUSSION

Potential distribution of *A. gracilipes*

A. gracilipes is a dangerous invasive species for indigenous animals, and its origin and possible global pattern of invasion need to be determined. Based on the potential ranges of expansion at different time scenarios using alternative modeling algorithms, six conclusions can be made.

First, the potential distribution under past, current and future climatic conditions suggests that *A. gracilipes* prefers warm and humid areas (Li *et al.* 2006). Ocean islands and peninsulas showed high risk to invasion from *A. gracilipes.* The Korean, Arabian and Iberian peninsulas, Sulawesi islands and Papua New Guinea were predicted to have a high invasive risk. It is clear from GARP that predicted climate change around the year 2050 will greatly increase the areas at risk of invasion by *A. gracilipes* compared to its current distribution. Under the current climatic envelope, the suitable distribution range may include the latitudinal area from 35 S and 35 N worldwide.

Under a 2050 climatic scenario, its suitable range could extend to more northern areas. Interestingly, the reconstruction of the ancestral potential distributional range of *A. gracilipes* in the middle Holocene showed that *A. gracilipes* favored high latitudinal zones.

Second, I employed ecological niche modeling to reconstruct the ancestral distributional range (Peterson *et al.* 2004; Yesson & Culbam 2006a) using three algorithms. This methodology may offer new insights into historical invasion dynamics. The results indicated that south Asia might have been the origin of diversification for *A. gracilipes* because two of the models (BioClim and Environmental Distance) have supported that *A. gracilipes* were mainly located in South Asia (high probability) in the early Holocene, whilst the Afrotropical zone was showed the low occurrence of the insect (Figs. 3B, C). The result of GARP in modeling ancestral distribution of *A. gracilipes* is not satisfied because the result map could cover most of the Afrotropical zone and South Asia (Fig. 3A), which make defining its origin difficult. Therefore focusing on the other two models, which produced more focused results may yield some insight. Output from BioClim and Environmental Distance indicated that suitable areas in south Asia in 6000 yr B.P. were almost kept constant to that of current model (Figs. 3B, C). Europe might have played the role as a bridge to transfer this insect to Africa in the early Holocene because it also has the occurrence probabilities in Europe, as supported by the three models (Figs. 3A, B and C). Based on these findings, I propose that the historical dispersal pattern of this insect took the following form: originating from south Asia, *A. gracilipes* first expanded to Europe and then transferred into Afrotropical regions. BioClim and Environmental Distance seemed to be better candidates when modeling past climatic scenario because they generated similar outputs under past climatic conditions. BioClim, along with Maxent model, have been successfully applied to construct ancestral niches for *Cyclamen* (Yesson & Culham 2006a, 2006b). GARP may not function as well in this area because the resulting output for *A. gracilipes* remained mostly unchanged from its current scenario.

Third, all three models supported a latitudinal shift of suitable distribution range for *A. gracilipes* under climate change scenarios. For example, in Australia, all models predicted the country will increasingly face a high risk of invasion (Figs. 2A, B and C); however, under the current climatic condition, the risk maps from all models did not include Australia.

Fourth, Wetterer (2005) proposed that the rainforest areas of the world would be suitable areas for this insect

based on empirical observations; whilst my study illustrated the finer resolution of potential range using alternative mathematical modeling techniques. My modeling results were consistent with those of Wetterer (2005), but generated more suitable areas for *A. gracilipes*. In the present study, the ant was not only shown to invade tropical forests, but also had suitable ranges in temporal ecosystems, for example south China, southeastern areas of the US and the Himalayas (Figs. 1A, B and C).

Fifth, I suggest that the high susceptible areas for this insect are mainly Australia, Asia, Africa and South America. Areas that have high biological diversity should be focused upon in order to prevent this insect from being introduced. The complexity of ecosystems in biodiversity hotspots (Myers *et al.* 2000) provide composite ecological conditions for the propagation of exotic species; therefore, the controlling strategy and risk assessment of biodiversity hotspots might be helpful in the management of this ant species. This is a potential implication of ecological niche modeling to invasive pest controlling, because we could readily identify the overlapping regions between important conservation areas (typically biodiversity hotspots) and the predicted highest risking areas, and correspondingly set up new monitoring strategies.

Sixth, although I have presented the prediction from three climatic sequences using three algorithms, I acknowledge that it is still difficult to determine a final future scenario. Lester (2005) argued that New Zealand was too cold to allow the permanent establishment of *A. gracilipes*. However, in the present study, parts of New Zealand are predicted as suitable for the survival of the insect, despite the probability not being high (Figs. 1A, B and C). A similar situation also occurs in Australia. The Australian Government (2006), has predicted that northern and eastern parts of Australia are suitable for this ant; however, my modeling did not predict the occurrence of *A. gracilipes* in Australia under current climatic conditions. One possible reason for this discrepancy is the influence of environmental variable selection (Heikkinen *et al.* 2006; Poyry *et al.* 2007) as selecting different environmental layers in building models would significantly affect the final output. Each environmental variable has its own characteristics and often the correlation between these is not strong, this leads to differences in the model-building process between studies.

Limitations of the present study

One possible limitation of the models under three climatic scenarios is a violation of the 'niche conservatism'

hypothesis (Wiens & Graham 2005; Hoffmann 2005; Yesson & Culham 2006a, 2006b). Biotic interactions, evolutionary change and environmental disorders may disable niche conservatism (Araujo & Luoto 2007; Fitzpatrick *et al.* 2007) and therefore lead to uncertainty of ecological niche modeling in ancestral niche and future climatic change modeling. Generally, the dramatic environmental change events will significantly cause the disorder of niche conservatism and invalidate ecological niche modeling. A recent typical example is the snow damage that occurred in China late 2007. Some mammalian species in southern provinces are now thought to be extinct due to the extreme cold temperatures experienced during that time (Wildlife Conservation Society China Program 2008). This exemplifies the uncertainty of niche conservatism and the unpredictability of past and future models. However, when the aim is to predict a course of potential distribution at a global scale, some environmental disorders and biotic interactions at lesser regional scales can be ignored.

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