

**Potential Geographic Distribution of *Anoplophora glabripennis*
(Coleoptera: Cerambycidae) in North America**

ABSTRACT.—The potential for ecological and economic damage caused by invasive species is only beginning to be appreciated. A recently arrived, and particularly worrisome, invader in North America is the Asian longhorned beetle *Anoplophora glabripennis* (Motschulsky), the larvae of which damage trees and forests. The geographic extent and likely path of its possible invasion of North American forests, however, are unknown. Herein, we develop and test ecological niche models for the species based on features of climate from the species' native distribution in eastern Asia, and then project them onto North America to identify areas of potential distribution. These models suggest that the species has the potential to invade much of eastern North America, but only limited areas in western North America, and that a focus of initiation of invasions is likely to lie in the area south of the Great Lakes. This result is particularly clear under modeled scenarios of spread and contagion.

INTRODUCTION

The existing approach to combating species' invasions is largely reactive in nature: strategies are generally developed for a species once it has been detected as an invader, and potential for invasion is evaluated via retrospective analysis of previous cases (Lawton and Brown, 1986; Carlton, 1996). This reactive nature to understanding potential invasiveness means that combating invasive species will usually prove enormously challenging. Recently, however, new approaches from multivariate statistics, quantitative geography and biodiversity informatics have been applied to the challenge and predictive models of species' invasions have been developed (Panetta and Dodd, 1987; Podger *et al.*, 1990; Honig *et al.*, 1992; Richardson and McMahon, 1992; Sindel and Michael, 1992; Scott and Panetta, 1993; Reichard and Hamilton, 1997; Higgins *et al.*, 1999; Sutherst *et al.*, 1999; Skov, 2000; Zalba *et al.*, 2000; Hoffmann, 2001; Peterson and Vieglais, 2001; NAS, 2002; Peterson *et al.*, 2003); these models have the potential to shift invasive species studies to a more proactive approach although the number of candidate invasives can end up being daunting.

The procedure employed herein (Stockwell and Noble, 1992; Stockwell, 1999; Stockwell and Peters, 1999) is an effort to create models of species' ecological niches in environmental dimensions based on characteristics of areas inhabited and not inhabited on or near native distributional areas (Peterson *et al.*, 2002b). This model is effectively a hypervolume in ecological dimensions (MacArthur, 1972) in the form of a heterogeneous set of rules; such models can be projected onto landscapes to predict geographic distributions (Peterson, 2001; Fera and Peterson, 2002; Peterson *et al.*, 2002a; Peterson *et al.*, 2002b; Peterson and Kluzas, 2003). When models are projected onto other regions, predictions can be developed regarding species' potential geographic distribution in not-yet-invaded regions; tests of this approach have yielded excellent predictivity (Peterson and Vieglais, 2001; Papes and Peterson, 2003; Peterson *et al.*, 2003a,b; Peterson and Robins, 2003).

The ecological niche modeling approach is closely allied to the body of work developed under the rubric of 'climate matching,' differing principally in the level of detail (and computer time) involved in developing models. Although this approach has been in general underappreciated (NAS, 2002) or ignored (Kareiva, 1996), it has, nevertheless, seen extensive testing with excellent results (Panetta and Dodd, 1987; Podger *et al.*, 1990; Richardson and McMahon, 1992; Sindel and Michael, 1992; Martin, 2001, 1996; Skov, 2000; Hoffmann, 2001; Welk *et al.*, 2002) and provides good predictivity as to the potential geographic course of species' invasions. It requires assumptions that: (1) the factors modeled on the native distribution of the species are indeed those that govern its distribution (and not just spuriously or indirectly correlated) and (2) that these same factors will act similarly in a different geographic and biological context. Although this approach does not provide precise predictions of which species will arrive and invade when and where, it does indeed hold predictive ability regarding one important component (geographic potential) of the invasion process (NAS, 2002).

Herein, we use known occurrences on a species' native distributional area and broad-scale climatic variation to predict the potential North American distribution of a particularly worrisome invading species, the Asian longhorned beetle (*Anoplophora glabripennis*). This species, which has appeared in warehouses in numerous cities across North America, was first discovered to have colonized trees in the United States in the late 1990s, particularly in the New York City and Chicago areas (Cavey *et al.*, 1998; Nowak *et al.*, 2001). Although considerable interest has focused on its physiology, ecology and possible biocontrol (Nowak *et al.*, 2001; Smith *et al.*, 2001; Bancroft *et al.*, 2002; Keena, 2002; Smith *et al.*, 2002), little or no research has assessed the geographic dimensions of its potential as an invader. Although one study provided an assessment of invasive potential in Europe (MacLeod *et al.*, 2002), no such examination has focused on North America.

METHODS

Ecological niches and potential geographic distributions were modeled using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Noble, 1992; Stockwell, 1999; Stockwell and Peters, 1999). In general, the procedure focuses on modeling ecological niches (the conjunction of ecological conditions within which a species is able to maintain populations) (Grinnell, 1917). GARP includes several distinct algorithms for niche modeling in an artificial-intelligence-based approach. Occurrence points are divided evenly into training and test data sets. GARP works in an iterative process of rule selection, evaluation, testing and incorporation or rejection: a method is chosen from a set of possibilities (*e.g.*, logistic regression, bioclimatic rules), applied to the training data and a rule is developed or evolved. Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, crossing over, etc. Predictive accuracy is evaluated based on 1250 points resampled from the test data and 1250 points sampled randomly from the study region as a whole. The change in 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.

A total of 40 occurrence records for Asian longhorned beetles was kindly provided for this effort by S. Lingafelter (U.S. Dept. of Agriculture) based on available specimen localities for the species from eastern and southeastern Asia (no control for type of collection site was possible, as these records represent what few could be assembled at the initiation of our modeling effort). This sample, while not large by any means, falls in a range within which predictive models can generally be developed (Stockwell and Peterson, 2002). Records were georeferenced by hand by Lingafelter and plotted in ArcView (version 3.1). Four localities identified as uncertain from the outset by Lingafelter constituted spatial outliers when plotted and were eliminated from analysis. GARP models were built based on 15 geographic coverages representing climatic dimensions drawn from ArcAtlas (ESRI, 1997): including high and low values for annual, January and July mean temperature and precipitation, solar radiation, snow cover and frost-free days. Coverages were imported into ArcView and exported as ASCII raster grids with 22×17 km pixels across eastern and southern Asia, and 1×1 km pixels across North America. All GARP analyses were conducted using a desktop version now available for download (Scachetti-Pereira, 2001).

To assess model quality, Asian longhorned beetle distributions were modeled in Asia based on half ("training points") of the known occurrence points and then model adequacy tested with the other half ("test points"). We chose equal partitions five times randomly and assessed success of the model in predicting the test data set, compared with success expected if points were distributed randomly, using a chi-square test. That is, the proportional area predicted present multiplied by the 20 test points provided expected numbers under a random model. To produce an overall "best" model, however, all 40 points available were used to develop 20 independent models based on the full data set; these maps were summed to produce a graded map of predicted presence with values ranging from 0 to 20. The 15 climatic coverages were combined with the summed GARP predictions using the "Combine" option (Arc/INFO, version 8.1). The associated attributes table of this composite coverage allowed visualization of modeled suitability vs. availability of combinations for key environmental dimensions.

Rule-sets associated with the 20 models for the Asian distribution of the species were used to identify areas in North America that fulfill the modeled ecological requirements of the species, thus predicting a potential geographic distribution in North America (Peterson and Vieglais, 2001). This geographic

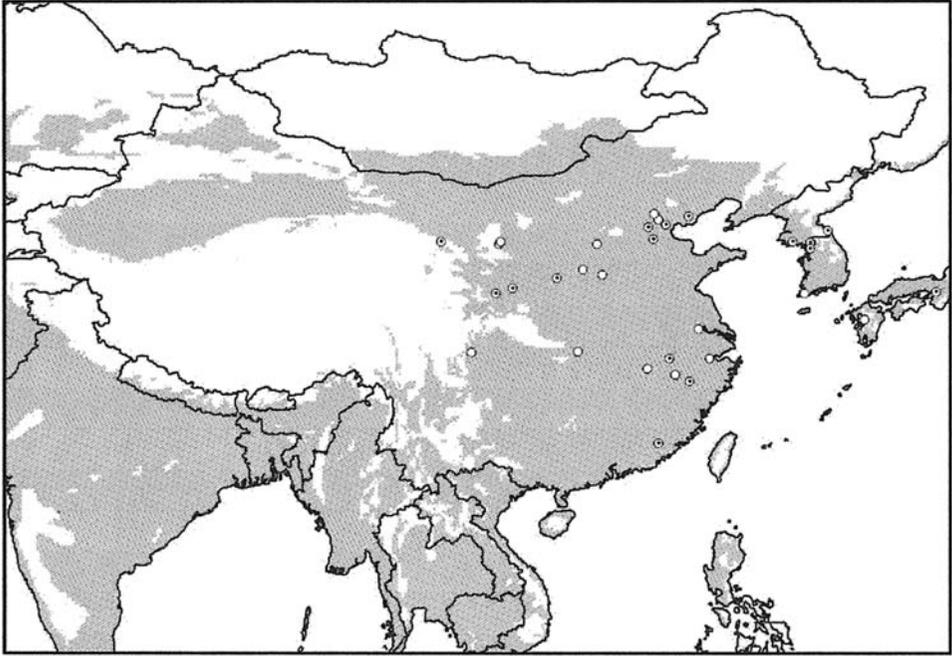
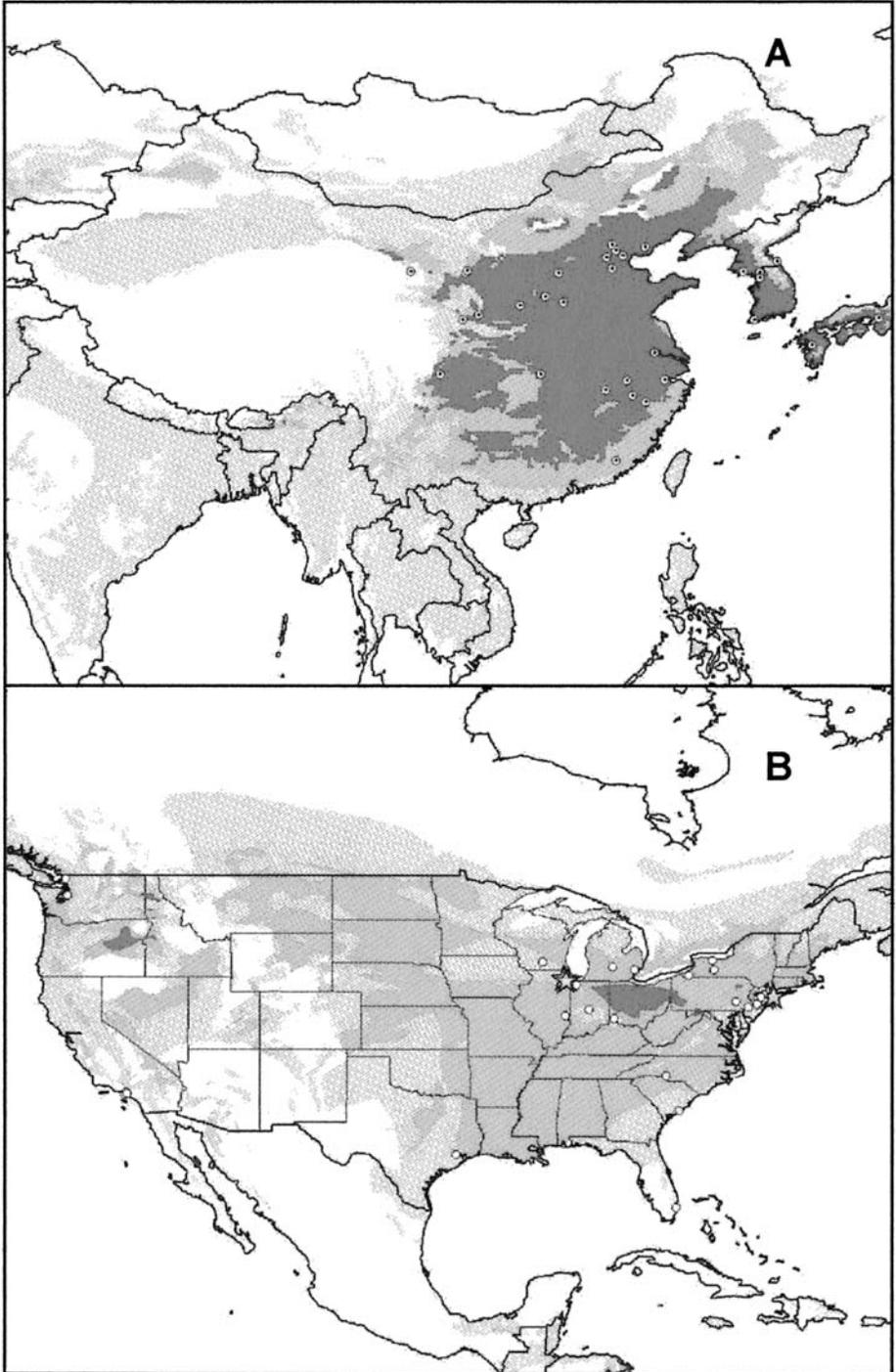


FIG. 1.—Example test of native-range model predictivity, showing a model based on 20 points chosen randomly for model building and 20 for model testing (dotted circles; not all visible owing to close proximity among some pairs of points). Significance of this iteration of the test, based on comparison with a random model, was $P < 3 \times 10^{-10}$. Gray areas are predicted present

prediction represents the conjunction of climatic conditions modeled as appropriate for the species on its native range projected onto the potentially invaded range.

Invasive spread was modeled using an adaptation of the Ecological Model for Burning the Yellowstone Region (EMBYR) wildfire simulation model (Hargrove *et al.*, 2000). This model (developed for modeling wildfire spread) provides an excellent parallel to species' dispersal—fires spread via ignition of adjacent areas and also through longer-distance dispersal by means of 'firebrands'—these two modes of spread constitute an excellent parallel to how an invasive species extends across a landscape. It is important to note that our parameterization of the EMBYR, which covered an order of magnitude of dispersal radii (see distance distributions below), is intended to assess the spatial pattern of invading populations rather than actual rates of spread. Hence, we initiated the EMBYR model at 32 points of known warehouse or tree infestation in North America; of these points, 28 fell within predicted potential habitat, which was reclassified in equal intervals to six suitability levels (levels 2–6 considered habitable, sending 2–6 beetle propagules to distant cells; at the distant site, beetle establishment

FIG. 2.—Geographic predictions for Asian longhorned beetles. (A) Prediction of potential geographic distribution of Asian longhorned beetles across eastern Asia. (B) Map of North America illustrating modeled suitability of climate regimes for Asian longhorned beetles, based on the model underlying (A). Dark gray = all models agree in predicting presence, medium gray = a majority of models agree in predicting presence, and light gray = at least one model predicts presence. Input occurrence points are overlain in (A) as dotted circles (not all visible owing to close proximity among some points); warehouse occurrences are shown in (B) as open circles; and known invasions of natural habitats are shown in (B) as stars



probabilities by habitat level were set at 0.065, 0.07, 0.075, 0.084 and 0.100, respectively; adjacent diffusive spread probabilities ranged 0.07–0.40 depending on suitability). Beetles were allowed to spread by “jumping” propagules to remote cells following a negative exponential distribution in random directions, as well as via adjacent diffusion. Each propagule experiences a stochastic chance of establishment based on habitat quality at the distant site. Spread is strongly dependent on the mean distance that propagules travel. We used negative exponential distance distributions with means of 0.1, 0.2, 0.3, 0.5 and 1.0 degrees. We stacked the results of 20 stochastic replications of each run to create risk maps showing spatial likelihood of beetle invasion. Simulations were stopped when infestation had spread across all predicted potential habitat.

RESULTS

Five random equal partitions of available occurrence data were used to test whether accurate and predictive ecological niche models can be developed for Asian longhorned beetles in climatic dimensions on geographic scales. For example (Fig. 1), all 20 independent test points were correctly predicted by the model, but only 33.2% of the region was predicted present, yielding an expected 6.6 correct predictions under a random model. This degree of coincidence was unexpected statistically ($P < 3 \times 10^{-10}$); the other four iterations of this procedure yielded significance values of $10^{-7} > P > 10^{-13}$. This result indicated that models developed for the species were indeed predictive of the species' ecological requirements and potential geographic distribution.

Next, we strove to develop an overall best model based on all data available. The GARP algorithm's random-walk approach to model development produces variation from one run to the next, yet certain areas are predicted present consistently, and others predicted present in few or no models (Fig. 2A). This map thus illustrates a range of confidence in likelihood of occurrence from low to high. Translating this geographic prediction into ecological space, patterns of ecological limitation were clear in most climatic dimensions (*e.g.*, precipitation and temperature; Fig. 3).

The rule-sets associated with the 20 Asian models were used to identify areas in North America that fulfill the modeled ecological requirements of the species (Fig. 2B). Patterns of low probability (arctic regions, high montane regions), intermediate probability (northern regions, western North America, Mexico and Central America), and high probability (eastern North America) were clear, suggesting that the species would encounter vastly different suitabilities of climate regimes at points across North America. This map was compared with a sample of known warehouse detections and actual outbreak distributions in North America (APHIS, 2003). Coincidence with warehouse detections was poor (chi-square test, $\chi^2 = 0.34$, $df = 1$, $P > 0.05$), suggesting that these occurrences are more related to opportunity for arrival than to the suitability of the site for the species. Actual infestations, however, appear to be predicted better: both major sites (Chicago and New York) are within the general prediction of 75% of models, but are too few to attempt statistical testing.

This habitat suitability map (Fig. 2B) summarizes potential habitat for Asian longhorned beetles, but does not discern which parts of this potential range are reachable by the beetles (Peterson *et al.*, 1999). The EMBYR model permitted us to investigate the spatial pattern of invasive spread from known warehouse entry points. The resulting maps (Fig. 4), which take into account both potential habitat suitability and opportunity for invasion, highlight the Great Lakes region as a critical center of initial invasion. All runs of the epidemic model showed the same general pattern of initial invasion in the Great Lakes region and left patches of optimal climate in eastern Oregon uninvaded; such unreachable areas of suitable habitat were insensitive to variation in model parameters although additional invasion points (warehouses) might alter this result. The beetles spread to maximum extent in all simulations within 120 generations; simulations assuming larger dispersal distances took fewer generations.

DISCUSSION

The models presented here, although constituting a ‘second generation’ (Peterson and Vieglais, 2001) of application of our modeling tools to the question of potential Asian longhorned beetle distributional areas in North America, remain provisional for a number of reasons. Model validations are based only on native distributional areas which may not be indicative of model predictivity in North America—fortunately, data for a test of model predictions in North America do not yet exist! Moreover, the implications of type of infestations represented among the native-range data from Asia are

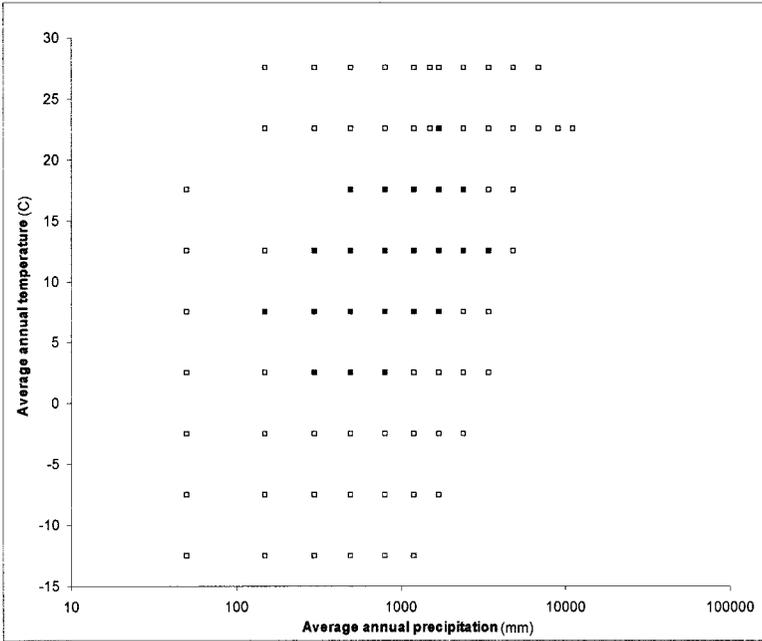


FIG. 3.—Plot of annual mean temperature *versus* annual mean precipitation, showing availability of environmental combinations across eastern Asia (open squares) and those predicted present in all 20 models for Asian longhorned beetles (closed squares). Note that each temperature-precipitation combination represents many combinations with other climate variables (*see* Methods) and that some combinations include both presences and absences, depending on values of other climate variables

unexplored—a very interesting analysis would be to compare ecological niche characteristics of natural populations with those of populations that are in epidemic proportions and causing damage in anthropogenic landscapes, particularly as relates to monospecific tree plantations in China and irrigation regimes.

The EMBYR models used herein to mimic dispersal processes provide a useful means of integrating the potential geographic distributions that are the output of ecological niche modeling algorithms into the more realistic picture of actual distributional areas, which are reachable by dispersing individuals. Although not as advanced as some implementations of such dispersal models (Clark *et al.*, 2001), this simple approach that is clearly adaptable to the question at hand gives a first-level answer to how dispersal can interact with climatic suitability. Clear next steps would be integration of more realistic dispersal parameters into dispersal models (Smith *et al.*, 2001), as well as introduction of density-dependent factors into consideration.

We compared our climate-based maps with a risk map developed by the U.S. Forest Service based on forest types known to be vulnerable to the species in its native range (Anonymous, 2003). This latter map emphasizes the northeastern fringe of the United States from Minnesota to Maine, whereas our results focus somewhat farther south. However, many of the same tree species (*e.g.*, maple, elm, birch) on which the Forest Service map focused are planted as ornamentals and shade trees far south of their native range, in cities and towns throughout eastern North America. Hence, even in the absence of vulnerable native forest, climatic conditions are appropriate for the species throughout much of the eastern United States and southeastern Canada and appropriate tree species are available. This result is, in some respects, similar to the climate-matching assessment of the species' potential distribution in Europe (MacLeod *et al.*, 2002), in showing a discord between the distributions of appropriate host plants and the appropriate climatic conditions for the beetles. Our predictions do require the assumption of no evolu-

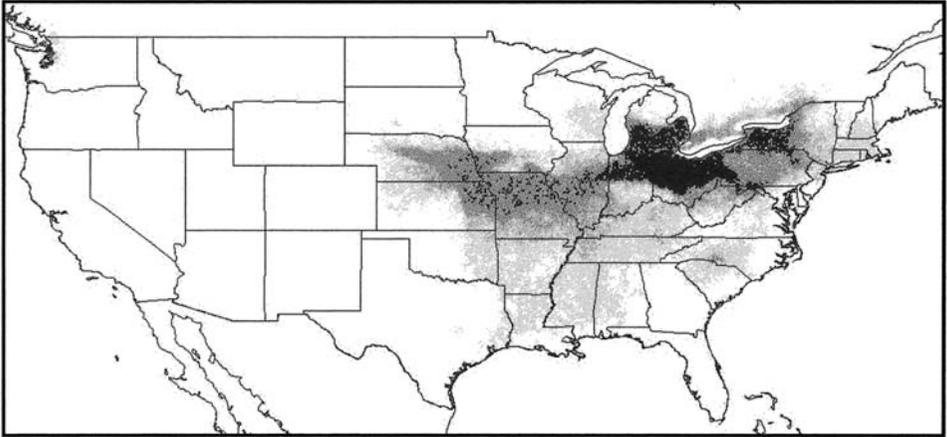


FIG. 4.—Map of invasive spread of Asian longhorned beetles in North America, developed via an epidemic simulation model and based on suitability of habitat modeled using GARP (Fig. 2B), with invasions starting at known points of presence in North America and likelihood of invasion represented by increasingly dark shades

tion in niche characteristics of the species during the invasion. Although niche evolution is generally conservative over such time spans (Peterson *et al.*, 1999), this assumption must be borne in mind.

Our analyses suggest that the area of greatest danger of Asian longhorned beetle invasion in North America is not, as might be expected, along the west coast, where Asian shipping volume is greatest. Rather, the eastern portion of the country is most vulnerable because abundant appropriate habitat lies close to major shipping ports. Although danger does still exist from secondary transportation (*e.g.*, by truck or rail) in the west, the clear priority for combating this invasive insect species is in the east, particularly the area just south of the Great Lakes. Modeling suitability of habitat combined with opportunity for invasion allows mitigation efforts to be concentrated in areas most vulnerable to invasion and may save time, effort and money, as well as improving possibilities of successfully combating the invasion.

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