Articles

Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack a Pressing Problem

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On **3 February 1999, President Clinton signed an** executive order dealing with invasive species in the United States. The order was designed to lay the foundation for a program "to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause" (Clinton 1999). This program includes far-reaching plans to prevent, plan, monitor, and study species' invasions. Such high-level attention emphasizes the enormity of the problem facing the United States, and in fact the entire world: With ever-growing international commerce, reduced barriers to trade, and increasing human influence, species are moving around, and natural systems are suffering drastic changes.

The dimensions of the problem are indeed impressive. Alien plants, animals, and microbes have poured into the United States from all directions. Natural systems have been disrupted, species extinguished, transportation and agriculture compromised, and resources damaged (Carlton 1997–1998, Ogutu-Ohwayo 1997–1998, Richardson 1997–1998, Shiva 1997–1998). In fact, most modern agriculture is based on nonnative organisms; problems arise because questions of when and why some escape and become nuisances remain unanswered. More generally, no proactive approach to combating such species is available—invasive species are dealt with one at a time, as they become problematic.

Scientific approaches to a synthetic, and ultimately proactive, understanding of species invasions have developed along several lines, but most have been frustrated by the complex and unpredictable nature of such invasions—which species will invade and which invaders will become serious problems? For example, considerable effort has gone into identifying characteristics of species likely to invade, or of invaders likely

A NEW APPROACH TO ECOLOGICAL NICHE MODELING, BASED ON NEW TOOLS DRAWN FROM BIODIVERSITY INFORMATICS, IS APPLIED TO THE CHALLENGE OF PREDICTING POTENTIAL SPECIES' INVASIONS

to become pests (e.g., Lawton and Brown 1986, Smallwood and Salmon 1992, Carlton 1996). Another line of inquiry and effort has focused on modeling spatial patterns of range expansion after initial invasion (e.g., Mollison 1986, Williamson and Brown 1986, Reeves and Usher 1989, Hastings 1996, Shigesada and Kawasaki 1997, Holway 1998). All in all, though, a general, synthetic, predictive, proactive approach to species invasions is lacking (Mack 1996) but is desperately needed (Hobbs and Mooney 1998).

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Existing approaches to the challenges presented by species invasions are reactive in nature, and for that reason they will always be trying to catch up to the most recent problem. Species that have managed to invade a particular region become the focus of intense activity and attention, and solutions—usually in the form of control measures and abatement—are designed to eradicate the species. This scenario, however, does not prevent other invasions.

The various scientific models of species' invasions that have been developed address dispersal capabilities (the possibility of invasion), population biology of invading species (i.e., population dynamics at small numbers), and the spatial dynamics of invasion (i.e., the diffusion of invading populations across a landscape). In this article we explore the applicability of new tools from biodiversity informatics and quantitative geography to another approach, one that builds on pioneering efforts by Higgins et al. (1999) and Zalba et al. (2000) and focuses on identifying portions of a landscape that are habitable for the invading species.

Information on geographic distributions in the form of primary point occurrence data (Peterson et al. n.d.) is harvested from new biodiversity information sources, niches of species are modeled in ecological space, and niches are projected onto potentially invaded landscapes. The advantage of this modeling procedure is that the possibility of an invasion can be assessed before the actual introduction of the species, as is illustrated herein by means of four case studies. Given that introductions and the negative effects of a particular invasion are difficult to predict, we outline a way to build biota-wide sets of projections to examine risks of species invasions for all species from a particular region. Thus the reactive nature of current solutions is replaced with a proactive, predictive approach.

Niche conservatism and historical determination of range limits

The impressive ability of species to invade areas outside their native distributions is founded in the evolutionary characteristics of ecological niches—the set of environmental factors that determine where a species can and cannot maintain populations—and in their relation to current geographic distributions. Recent theoretical modeling efforts have demonstrated that species' ecological niches are likely to evolve only slowly and under circumscribed conditions (Holt and Gaines 1992). These predictions are amply supported by empirical data: Thirty-seven pairs of sister species of birds, mammals, and butterflies, isolated from one another in southern Mexico for 10^5 to 10^6 years, had statistically significant similar niche characteristics (Peterson et al. 1999). Hence, species' ecological niches generally appear to be stable over evolutionary time periods, an observation that is important for many of the arguments and ideas in this article.

Evolutionary stability in species' niche characteristics permits further inferences. Niche models define ecological limitations in the dimensions in which the model is developed. Consequently, a species' present geographic distribution can be projected via ecological niche models into geographic dimensions to predict where the species will and will not be able to maintain populations. However, a common observation is that predicted geographic distributions are too broad, extending into similar environments in adjacent or distant biotic regions (Peterson et al. 1999). Why might ecological considerations fail to explain so much of species' distributions?

A simple illustration of this phenomenon is that hummingbirds are found in the Neotropics, but not in the Afrotropics or in Southeast Asia. Without hesitation, most ecologists and systematists would agree that hummingbirds evolved in the New World and have never had the opportunity to invade the Old World. This explanation is historical in nature. As a contasting example, the horned guan (*Oreophasis derbianus*) is found in cloud forest, but not in adjacent tropical dry forest or cornfields. Here, it seems easy to conclude that the horned guan's niche does not extend to those other habitats—an ecological explanation. Inspection of large numbers of such predicted geographic distributions has shown that areas of overprediction frequently coincide with the presence of geographic and biogeographic barriers, suggesting that historical limitation is often a dominant factor in defining species' ranges (Peterson et al. 1999). Hence, we argue that widespread overprediction in projecting niche models onto landscapes is attributable in large part to historical factors that limit species' geographic distributions at medium to large spatial scales.

That historical factors largely determine species' geographic distributions offers a critical lesson about species invasions. Species with current distributions that are limited by historical factors will, if transported to a new region, often encounter areas with ecological conditions conducive to the species' survival. This inference is the critical point in this article: Ecological niches are stable and determine the set of possible conditions under which a species is able to invade a particular region.

Availability of biodiversity information

The approaches developed in this article depend critically on the availability of sufficient distributional information on which to base modeling efforts. The techniques we discuss rely on point occurrence information—records, usually in the form of specimens in a scientific collection, that place a particular species in a particular place (Peterson et al. 2001). Such data do exist, but the system under which they are maintained is widely dispersed and constrained by institutional and national boundaries. Although most members of the biodiversity community are willing to provide information, the existing arrangement is inefficient and difficult to access. For this reason, many studies such as those outlined in this article have not taken full advantage of existing information.

Most biodiversity information is stored in the form of scientific collections across North America and Europe. This information is often not computerized, and it is considered the property of individual institutions. Hence, access to each

collection must be obtained separately, making access to the totality of information a laborious task.

Using ANSI/NISO Z39.50, a standard for information retrieval that has proven successful in the bibliographic and geospatial domains, and the newer XML language, we have developed technology to overcome these impediments by permitting search and retrieval of information from biological collections connected by the Internet. The North American Biodiversity Information Network (NABIN) is a consortium of institutions from Canada, the United States, and Mexico, created and supported by the Commission for Environmental Cooperation in Montreal. NABIN and the National Science Foundation have supported development of the Species Analyst, a set of software extensions that enables distributed searches to be conducted: Users may query the databases of multiple collections simultaneously and, in a matter of seconds, extract information in a form suitable for further analysis. An additional component of the data network is a mechanism providing access to niche-modeling programs located on high-performance computing facilities at the San Diego Supercomputer Center.

Species Analyst thus provides an infrastructure that allows seamless search, retrieval, and analysis of a wealth of biodiversity data that has hitherto been impossible or impractical to use. The network includes data from 13 institutions on diverse taxonomic groups (Table 1). Among institutions slated for inclusion by the end of 2001 are the Field Museum (birds), Academy of Natural Sciences (birds, fish), Smithsonian Institution (fish), and the US Breeding Bird Survey. (See the Web site *speciesanalyst.net* for online access to the Species Analyst data network.)

Conceptual background

Our approach centers around the concept of ecological niches of species. The *niche*, as we use the term, is a set of tolerances and limits in multidimensional space that define where a species is potentially able to maintain populations (Grinnell 1904, 1917). Given the spatial scale of our analyses, we focus on niche dimensions relevant to geographic distributions

rather than to local distributional issues such as microhabitat or substrate selection. The niche dimensions modeled are therefore those usually considered in geographic limitation of species—temperature, precipitation, elevation, vegetation, and so on. These ecological requirements are generally divided into fundamental and realized ecological niches, with the former representing the base ecological capacity of the species and the latter incorporating the effects of interactions with other species (MacArthur 1972). Because community composition varies greatly over space, its impacts should vary as well (Dunson and Travis 1991). Models at the level of entire species' distributions may allow identification of broader ranges of environments potentially suitable for a species, roughly analogous to a fundamental niche, although on a coarse spatial scale. Predictive models are developed through a three-step process: (1) modeling niches in ecological space, (2) evaluating these niche models based on native distributions, and (3) projecting the models to areas that could be invaded.

Modeling niches. This first step in the procedure involves development of a multidimensional view of the ecological niche of a species, a considerable challenge given the complex nature of species' niches (Peterson and Vargas 1993). Early steps in this direction included the application of logistic regression to prediction of presences and absences (e.g., Mladenoff et al. 1995), as well as the development of the frequency distribution–based BIOCLIM approach (e.g., Nix 1986), among others. These approaches all suffer from two sorts of error: omission (leaving out niche space that is really occupied by the species) and commission (including niche space not actually occupied by the species). Each algorithm for modeling species' ecological niches involves a specific combination of errors of omission and commission.

A relatively new approach, called the Genetic Algorithm for Rule-set Prediction, or GARP (Stockwell and Noble 1992, Stockwell and Peters 1999), offers a better solution. Individual algorithms with diverse predictive approaches (e.g., multiple regression analysis to predict the probability of presence

Table 1. Summary of data sets available in Species Analyst (Web site speciesanalyst.net). Note that additional data sets, principally herbaria, are served via integration with the distributed server setup by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad in Mexico City (www.conabio.gob.mx).

Institution	Taxa
Royal Ontario Museum	Birds
Universidad Nacional Autonoma de México	Birds, mammals, lepidoptera
Arizona State University	General holdings, plants, lichens
University of Kansas Natural History Museum	Birds, mammals, fish, reptiles, amphibians, plants, insects
Museum of Vertebrate Zoology, U Cal Berkeley	Birds, mammals, reptiles, amphibians
California Noxious Weed Control Projects Inventory	Plants
University of Florida	Fish
Museum of Comparative Zoology, Harvard	Fish
University of Michigan Museum of Zoology	Fish
Tulane University	Fish
Environment Canada	Frogs
California Academy of Sciences	Reptiles, amphibians
Agriculture Canada	Lepidoptera

Predicting Geographic Distributions

Data from the US Breeding Bird Survey were used to build an ecological model for, and predict the geographic distribution of, the brown thrasher (*Toxostoma rufum*). For this example, data from 30 randomly chosen states were used to develop niche models (black; 1611 points), and data from remaining states (gray; 741 points) were used to test predicted distributions. Of test points, 707 were correctly predicted, as compared with 290 expected by chance; the probability of such accurate prediction by chance alone is less than 10^{-200} (Peterson n.d.). Overprediction in the Southwest coincides with distributions of congeneric species (see Peterson et al. 1999).
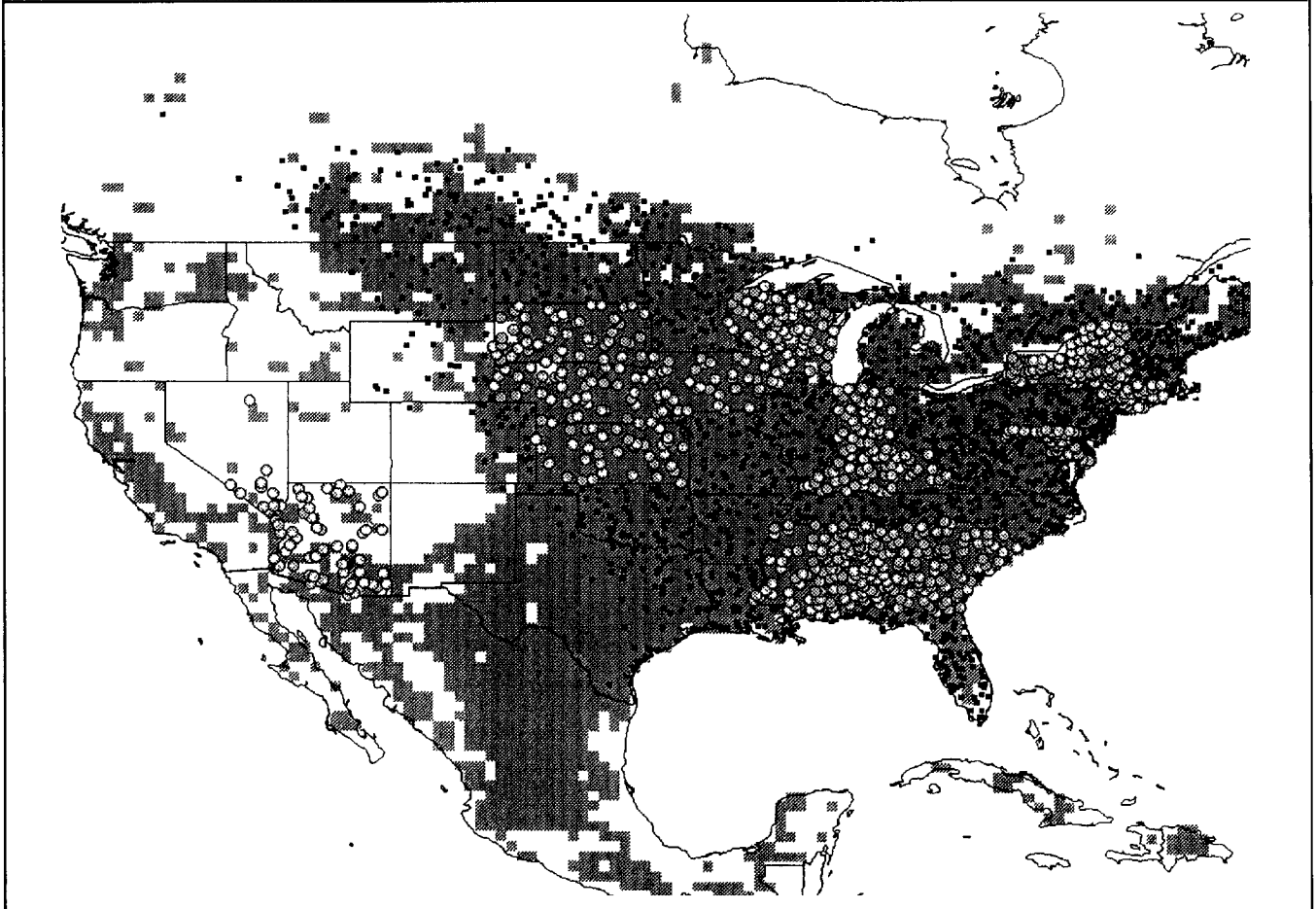
or the intersection of ranges along environmental dimensions) are used flexibly through many generations of rule modification, testing, and incorporation or rejection. Rule fitness— that is, predictive accuracy—is tested by comparing sets of points resampled from known occurrence points and from the background. The result of the genetic algorithm is a set of 5 to 50 different rules that together define the dimensions of the species' ecological niche. Tests of GARP have shown that it simultaneously reduces errors of both omission and commission, and hence provides a qualitatively better estimate of the actual limits of the species' ecological niche (Peterson et al. 2001, Peterson n.d., Peterson et al. n.d., Stockwell and Peterson n.d.). The rule sets describing ecological niches can then be projected onto GIS coverages for regions of interest (see the box above) to predict geographic distributions.

An implementation of GARP is accessible over the Internet at the San Diego Supercomputer Center (Web site *biodiversity.sdsc.edu/cgi-bin/BSW/screen.cgi*). To facilitate application of GARP to diverse geographic regions, several sets of environmental data (coverages) are available; although content varies from region to region, typical geographic themes include precipitation and temperature (averages and extremes), vegetation, elevation, slope, aspect, and soil type. In particular, fine-resolution data are available for the United States, North America, Mexico, Australia, West Africa, Canada, Maine, and China, and a coarser-resolution data set is available for global coverage. At the Web site users can paste geographic coordinates of species' occurrence points into a form, set model parameters, and run GARP to build an ecological niche model that identifies habitable ecological space; that

model can be used to predict distributions in regions where the species has not yet invaded. Analytical results can be presented as sets of model rules, map images, and ASCII grids readable by GIS (geographic information systems), making the data usable in a variety of applications. A desktop version of GARP, specifically tailored to facilitate diverse applications of the methodology such as that developed herein, is in a beta-testing stage (Ricardo Scachetti [University of Kansas Natural History Museum], unpublished data, 2001), soon to be released publicly.

Testing models. GARP models have been put to several tests for robustness and accuracy. Initial tests assessing robustness to variation in density of environmental data (Peterson and Cohoon 1999) and occurrence data sample size (Stockwell and Peterson n.d.) indicated that 4–8 environmental data sets and 10–30 occurrence points are generally sufficient to achieve maximum predictive accuracy for a given species.

A general scheme that can be used to test GARP model predictions is that of setting aside random samples of known occurrence points prior to analysis. Training data are used as the basis for the model in GARP, and test data are then used to assess predictive ability (Fielding and Bell 1997). Test data (the sample set aside) can be overlaid on the prediction, and numbers of points successfully predicted compared statistically with those expected at random. These approaches can be used on the species' native distributional area to assure that the model has significant predictive power. GARP models provided highly accurate predictions (more than 90% of points correctly predicted) of test data, and were significantly more accurate than random in predicting independent test data points for 22 of 25 Mexican bird species (Peterson et al. n.d.) and all of 39 US bird species studied (Peterson n.d.).

Predicting invasions. The final step in the framework is to project the ecological model onto landscapes that could be invaded. That is, using the same set of ecological dimensions, the ecological niche model is projected onto the landscape of interest in the study. This step may or may not be testable, depending on whether the invasion has taken place or is yet to happen.

The models can be applied to the landscape of interest in several ways. With the present Web interface, the most direct (and most time-consuming) method is to apply the derived rule set manually to a parallel set of coverages in the test region. This procedure provides a prediction specifically in terms of the region of special interest. A simpler approach is to develop the ecological model on a set of coverages that extend across both the native and the potentially invaded regions; in this case, the GARP facility provides the prediction in the test region directly; however, depending on the diversity of the regions involved, this approach can reduce the inferential power of the approach drastically. The forthcoming desktop version of GARP provides much-improved possibilities for projection of GARP models onto alternative landscapes. When data on invaded areas are available—that is, when the

analysis is retrospective, taking place after the invasion has occurred—the predictive ability of the model is testable with the statistical approaches described in Fielding and Bell (1997).

Worked examples

The theoretical framework for application of ecological niche models to the challenge of predicting species' invasions outlined above is useful only to the degree that it provides reasonable predictions of real-world invasions. Here, we analyze four examples of real or potential invasions: two retrospective invasions for which statistical tests are possible, one invasion that is just beginning, and one that has not yet happened, but might.

Cattle egrets. Cattle egrets (*Bubulcus ibis*) were originally restricted to the Old World Tropics in Africa and southern Asia. A flock of this species, however, was blown across the Atlantic Ocean to northeastern South America in the 1950s, where a population became established (Telfair 1994). Cattle egret populations quickly spread throughout the New World Tropics, and north through Central America and Mexico into the southern United States.

We used 70 historical Mexican records (1958 through 1988) from Species Analyst and individual scientific collections (see "Acknowledgments") to test whether the spatial extent of US colonization by cattle egret populations could be predicted accurately. The ecological niche model for the species in all of North America was based on eight geographic themes, including aspects of vegetation, precipitation, and temperature (Peterson and Cohoon 1999). We then tested the predictions of the model with 673 known occurrence points drawn from the results of the US Breeding Bird Survey (BBS) (Figure 1; Sauer et al. 2000).

The portion of this model extending into the United States predicts distributional areas across the southeastern states, extending narrowly along the Atlantic seaboard as far north as New York (Figure 1). The interior and western parts of the country are predicted either not to represent appropriate distributional areas or to hold only sparse populations. Overlaying the BBS test occurrence data on the model predictions, we found that the model predicted the areas invaded quite well: 57% of the country was predicted to be capable of supporting cattle egret populations, and 42.5% of US occurrence points were correctly predicted. Using chi-square tests to evaluate the significance of these predictions, probability levels for both were less than 10^{-200}, or impossibly successful unless the dimensions of the species' ecological niche were accurately evaluated.

House finches. This species, *Carpodacus mexicanus*, is native to western North America, ranging from the Great Plains west to the Pacific Ocean, and from southern British Columbia south to southern Mexico (Hill 1993). Introduced in 1940 into Long Island, New York, this species stayed for a long while in the immediate vicinity. In the 1960s, however, it began expanding rapidly throughout New England and south
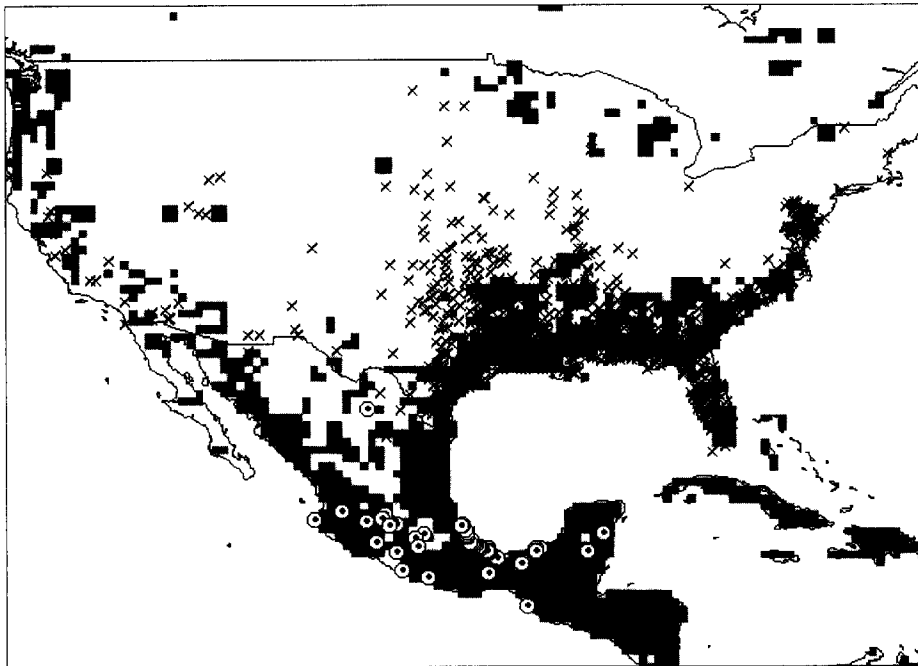
*Figure 1. Map of North America, illustrating predictive modeling of cattle egret (**Bubulcus ibis**) invasion. Circles represent training data (occurrence points from Mexico as the species invaded northward); in gray is the prediction developed; and black X's represent test data overlaid on the prediction.*
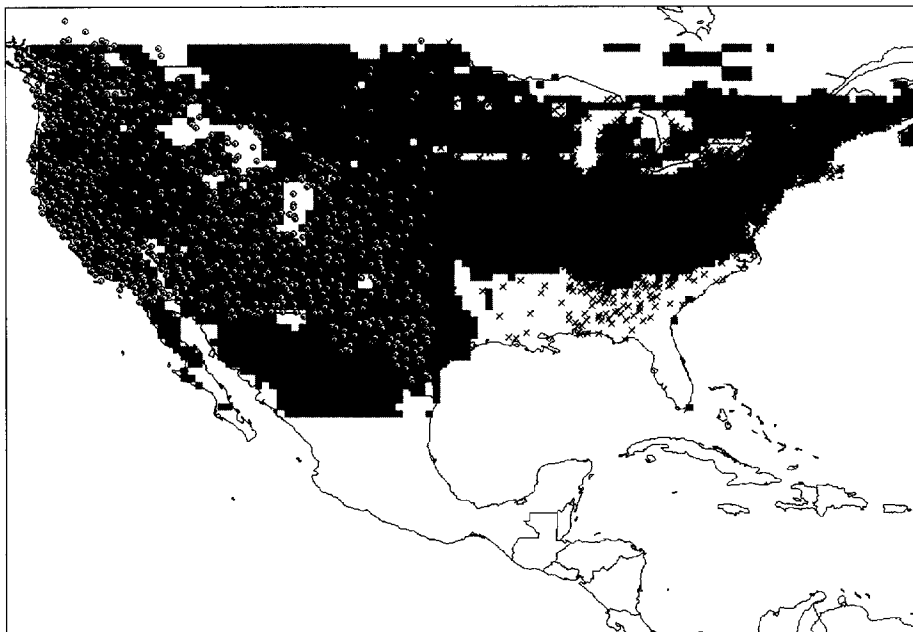

*Figure 2. Map of the United States, illustrating predictive modeling of house finch (**Carpodacus mexicanus**) invasion of the eastern portion of the country. Circles represent training data (occurrence points from BBS data for western North America); gray represents the distributional prediction for the native and invaded range; and X's represent the test data (occurrence points from BBS data for the invaded range).*

and west through much of the eastern United States. Eastern and western populations met in the eastern Great Plains in the late 1980s. The species' distribution appears to have been relatively stable since that time (Hill 1993).

We used 1333 occurrence points available through Species Analyst to establish ecological characteristics of the species in its native distribution in the western United States. Models developed (Figure 2) predicted most of the concentrations of 883 independent BBS records on the native range, achieving a fair degree of statistical significance ($X^2 = 23.4$, df $= 1$, $P = 1.3 \times 10^{-6}$), so our ecological model was successful in predicting the species' native distribution. Indeed, portions of western North America predicted by our model to hold populations but not corroborated by test data points (e.g., most of Montana) are now being invaded by populations of house finches (Hill 1993).

Applying the model to eastern North America, although only 28.6% of eastern North America was predicted to be suitable for house finches, the model correctly predicted 49% of the 1333 test data points. Chance alone is unlikely to account for this level of accuracy, with probability levels below 10^{-55} ($X^2 = 248.1$, df $= 1$). Hence, our model provides a much-improved idea of where this species was likely to invade in eastern North America.

Asian longhorn beetles. This species (*Anoplophora glabripennis*), featured recently in numerous news items in popular publications, is becoming a major pest in North America. Its native distribution extends across China, Japan, and North and South Korea (Figure 3a), where it is already a serious pest. Its larvae infest hardwood trees and bore large holes, making the wood useless for commercial production (e.g., in orchards) and weakening the trees' resistance to other diseases. The Asian longhorn beetle, although a pest in its native range, is of special concern in North America, given the possible absence of biological controls on its distribution.

Apparently arriving as an unwanted passenger in wooden pallets used for international shipping, this species has now appeared in warehouses in at least 46 sites across North America. It has managed to escape and infest two regions (Chicago and New York City and their environs). Control efforts have relied on removal of all trees in affected areas, clearly a drastic step.

Figure 3. Predictive modeling efforts for the Asian longhorn beetle (Anoplophora glabripennis). **(a) Distributional points and modeled distribution in southern and eastern Asia, and (b) potential distribution in North America, based on the Asian model.**

Modeling this species' native distribution illustrates its broad distribution across eastern and southeastern Asia (Figure 3a), although the limited number of distributional points available (40) was not sufficient to allow tests of model adequacy on the native distribution. When the ecological niche model was projected onto North America, eastern North America was identified as a solid block of potential distribution for the species, as shown in Figure 3b (two known infestation points are in this area). Interestingly, the Pacific Coast, where most Asian ships arrive, is not predicted to be an area of potential distribution. Although the projections are preliminary and much more detailed modeling of the species' ecological niche is needed prior to application in the real world, these efforts illustrate how these methodologies could have important applications for on-the-ground combat against real or potential invaders. For example, if more detailed modeling efforts support the initial results, Asian shipping could be focused on the Pacific Coast, where danger of invasion by this species is low, and direct shipments to vulnerable areas such as the Atlantic seaboard could be avoided.
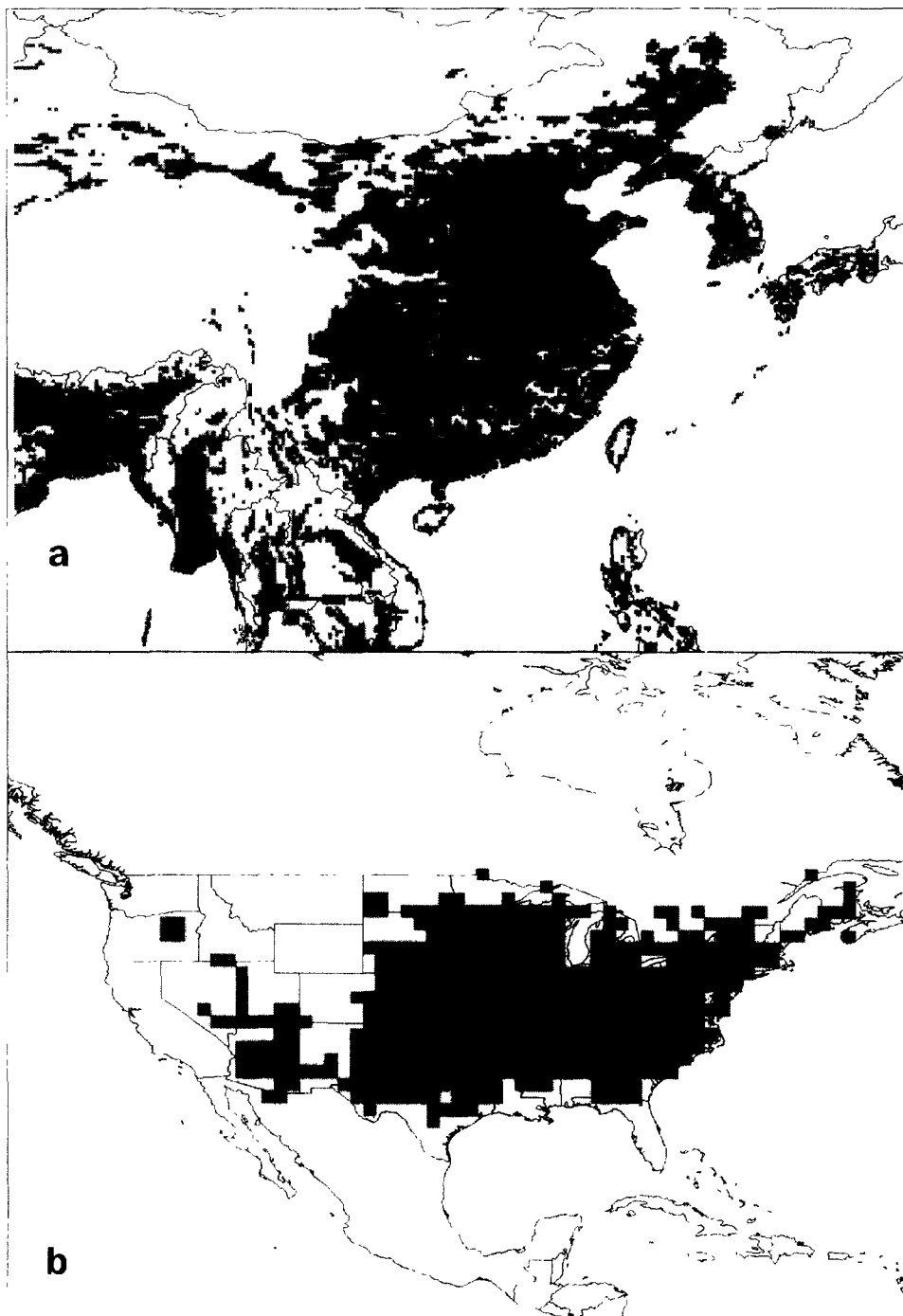
Japanese white-spotted citrus longhorn beetle.

This species is not yet invasive, but it merits careful consideration and analysis as a *potential* invader and serious pest. *Anoplophora malasiaca* Thompson is primarily a pest of *Citrus*; it is one of the major citrus pests in Japan (Japan Plant Protection Association 1981). Like the Asian longhorn beetle, it has a broad host range, including *Citrus, Salix, Morus, Melia, Pyrus, Platanus, Ficus*, and *Acer*, among others (Ohga et al. 1995). Adult activity, which runs from May to July and peaks in early June (Japan Plant Protection Association 1981), causes some damage to tree leaves. Larvae, however, bore through the wood of the tree, causing great stress and injury during their full year of development before emergence as adults.
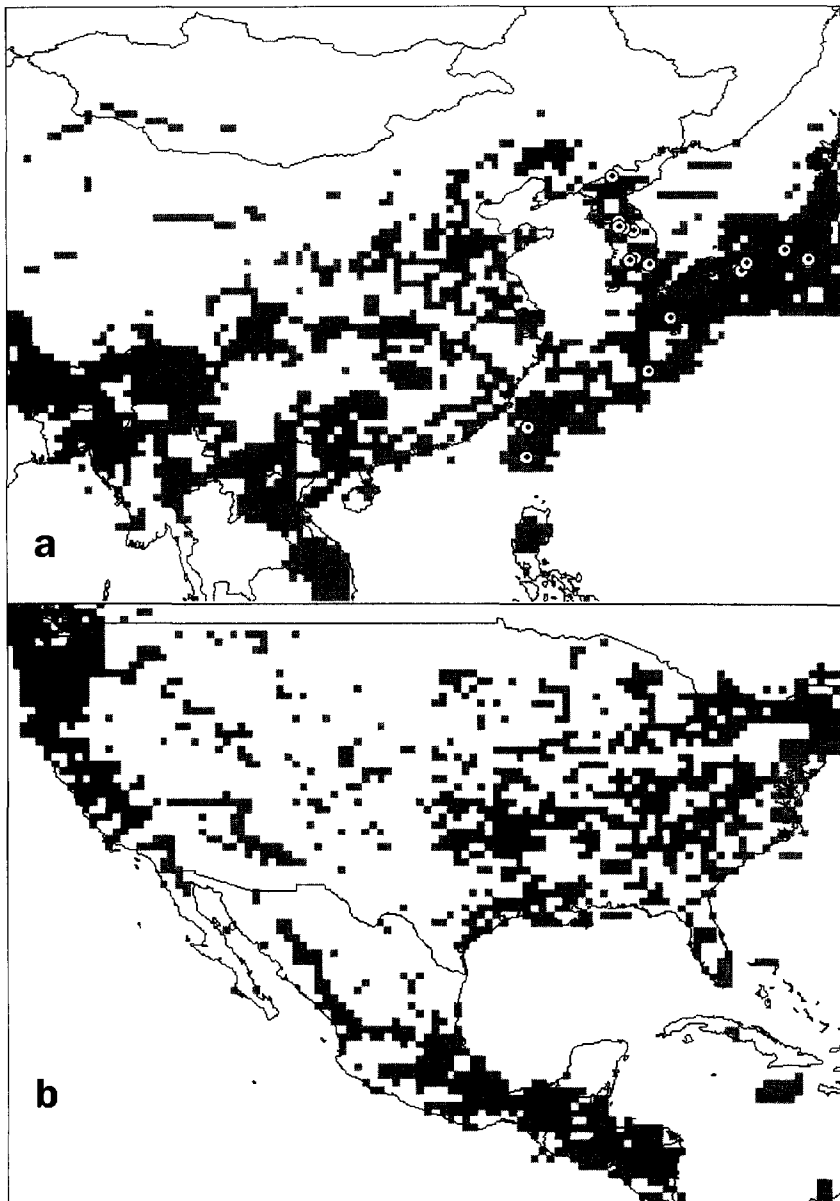
Figure 4. Distributional modeling efforts for the Japanese whitespotted citrus longhorn beetle (Anoplophora malasiaca). (a) Distributional points and modeled distribution in southern and eastern Asia, and (b) potential distribution in North America.

major *Citrus*-growing areas in California and the southeastern United States should raise concerns about the possibility and consequences of a future invasion.

[Note: Since this paper was submitted for publication, *Anoplophora malasiaca* has entered North America, having stowed away in the trunk of a bonsai tree, to appear in Wisconsin (see Web site *www.aphis.usda.gov/oa/pestaler/palbbn. html*). Although this appearance does not yet constitute an invasion, it certainly illustrates the potential for testing our suitability models via real, albeit unwanted, appearances of species in North America.]

Synthesis: Future possibilities

The theoretical framework for treating invasive species and the information infrastructure described above present fascinating opportunities for development of a proactive tool for invasive species risk assessment, namely, a virtual data facility. This facility, although computationally intensive, could create predictive ecological models for *all* species not native to a particular region. These models could then be used to develop strategies for avoiding species invasions that might result from certain activities, such as trading with a particular country or opening a new canal or transportation route. Such a facility could easily be incorporated into the activities of a number of agencies already focusing on invasive species.

Development of such a facility requires several strong steps. First, caretakers of biodiversity information will have to embrace the project, because they would have to share data that they might consider proprietary. It will require experimentation and exploration of new methodologies and approaches, in particular for the community of specialists in invasive species biology. Finally, it will require pushing the frontiers of technology to allow large-scale, fast computation for organismal biology, which calls for new algorithms and quick links with computer facilities that permit millions of complex analyses to arrive at a single result. This set of achievements would open the door to an entirely new, different approach to the invasive species challenge, one that is proactive, predictive, and quantitative.

Twenty-six distributional points from the species' native distribution in southern and eastern Asia were used to create an ecological niche model. Although occurrence points were insufficient to permit development of statistical tests, we projected this model across Asia to outline a potential native distribution (Figure 4a). Projecting the niche model to North America (Figure 4b), we were able to predict areas of potential invasion: across the southern United States, in much of central and southern Mexico, and spottily across the eastern United States. Given that this species constitutes such a serious pest of *Citrus* in its native distribution, the coincidence of its potential distribution with

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