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Time-specific ecological niche modeling predicts spatial dynamics of vector insects and human dengue cases

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Summary Numerous human diseases—malaria, dengue, yellow fever and leishmaniasis, to name a few—are transmitted by insect vectors with brief life cycles and biting activity that varies in both space and time. Although the general geographic distributions of these epidemiologically important species are known, the spatiotemporal variation in their emergence and activity remains poorly understood. We used ecological niche modeling via a genetic algorithm to produce time-specific predictive models of monthly distributions of *Aedes aegypti* in Mexico in 1995. Significant predictions of monthly mosquito activity and distributions indicate that predicting spatiotemporal dynamics of disease vector species is feasible; significant coincidence with human cases of dengue indicate that these dynamics probably translate directly into transmission of dengue virus to humans. This approach provides new potential for optimizing use of resources for disease prevention and remediation via automated forecasting of disease transmission risk.

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1. Introduction

Although the general geographic distributions of insect disease vector species are the subject of extensive monitoring and mapping efforts (Cooper et al., 2002; Shililu et al., 2003), the fine details

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can be obscure, even in such well-studied regions as North America (Levine et al., 2004). More importantly, however, within known geographic distributional areas of particular species, anticipating where and when they will emerge can be challenging. This contribution marshals a new suite of tools based in ecological niche modeling to the challenge of understanding spatiotemporal variation in the activity and geographic distributions of such unpredictable vector species.

Using this approach, known occurrences of species are related to ecological landscapes to produce models of species' ecological requirements. These models, when used to query landscapes to identify areas potentially habitable for the species, provide excellent predictivity regarding geographic distributions of species: distributions in unknown landscapes (Peterson and Kluza, 2003; Peterson and Shaw, 2003); species invasions (Peterson, 2003; Skov, 2000); climate change effects on species' distributions (Bakkenes et al., 2002; Midgley et al., 2003); and interactions among species in disease transmission cycles (Peterson et al., 2002b, 2003). However, to date, such models have used broad temporal averages in predictions, making them effectively blind to spatiotemporal dynamics. In this article, we explore and test the hypothesis that the details of spatial and temporal dynamics of vector populations and consequent disease outbreaks can be predicted via ecological niche modeling. In essence, this approach follows on from Pavlovsky's concept of natural nidi of infectious diseases (Pavlovsky, 1966), except that it tracks a moving target: vector mosquito populations that vary over both space and time.

2. Materials and methods

The overall analysis in this article involves distribution surveys of mosquito larvae used to predict month-specific distributions of these disease vectors. Secondly, we examine the correspondence between our predicted vector distributions and the geographic distribution of human dengue cases. The models we develop, in all cases, are tested based on independent suites of data, so the generality and predictive ability of models is assessed from the outset.

Ecological niche models were based on primary point-occurrence information (Peterson et al., 2002c) for *Aedes aegypti* drawn from larval surveys carried out across Mexico by the Laboratorio de Entomología, Instituto de Diagnóstico y Referencia Epidemiológicos (InDRE) Secretaría de Salud, Mexico. Samples were taken

monthly at points scattered across eastern and southern Mexico. Human case data were drawn from cases tested by InDRE for the appropriate period; exposure dates were calculated based on the assumption of an average of 18 days for onset of symptoms (including time to viremia in an infected human, extrinsic incubation in a mosquito, a second feeding on a human, intrinsic incubation in a second human, and time to viremia in the second human [see <http://www.cdc.gov/ncidod/dvbid/dengue/slideset/set1/i/slide04.htm>]) and 7 days between onset of symptoms and taking of sera for testing. Specifically, 181 mosquito distributional occurrences and 1994 human dengue case records for April–December 1995 were georeferenced using Mexican census data to the nearest 0.1' of latitude and longitude (Figure 1).

To characterize environments, we used seven Geographic Information System (GIS) coverages, summarizing aspects of the ecological landscape in Mexico (Figure 1). These coverages included elevation, slope, aspect and tendency to pool water (topographic index) from the USGS Hydro-1 K data set; and remotely sensed images, including monthly composite normalized difference vegetation indices (NDVI) for 1995 based on data from the Advanced Very High Resolution Radiometer (AVHRR) sensor. NDVI data were included in the modeling process as raw monthly composites, as well as differences between the particular month and the two previous months, for a total of three month-specific remotely sensed data layers. (Note that rainfall and other climatic information were not included, owing to the coarse nature of such data sets, which would not permit the fine-grained predictions developed in this article; regardless, rainfall is indeed reflected in the NDVI data via vegetational responses and increased or decreased photosynthetic mass.)

Ecological niche models were developed using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Noble, 1992), an evolutionary computing algorithm that has seen extensive testing for predictions of species' geographic distributions (Anderson et al., 2003; Egbert et al., 2002; Peterson and Cohoon, 1999; Peterson and Shaw, 2003; Peterson et al., 2004b; Stockwell and Peterson, 2002a, 2002b, 2003). GARP focuses on modeling ecological niches (the conjunction of ecological conditions wherein a species can maintain populations without immigration), relating ecological characteristics of occurrence points to those of points sampled randomly from the rest of the study region, developing a series of decision rules that best summarize factors associated with presence.



Figure 1 Monthly NDVI values from the AVHRR satellite for June–November 1995. Brown areas represent low NDVI values, whereas green areas represent high NDVI values. Comparisons among months illustrate month-to-month variation in conditions across Mexico. Occurrence data for *Aedes aegypti* are shown for each month as white squares.

Occurrence points are divided evenly into training and testing data sets. GARP carries out essentially the same general task as multivariate logistic regression, but its evolutionary-computing basis permits analysis of very complex data sets that would probably prove prohibitive for more conventional approaches. 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) and applied to the training data

to develop or evolve a rule. Predictive accuracy is evaluated based on the testing data. Rules may evolve in ways that mimic DNA evolution (e.g. point mutations, deletions). Changes in predictive accuracy between iterations are used to evaluate whether particular rules should be incorporated into the model; the algorithm runs 1000 iterations or until convergence.

GARP is a random-walk procedure, so it is necessary to take model-to-model variation into account, filtering out suboptimal models based on error

statistics (Anderson et al., 2003). This procedure, which was developed based on detailed comparisons with expert opinions of many replicate models, focuses the results on models that demonstrate independent test occurrence data, and thereby have predictive power. To this end, we developed 100 replicate models of ecological niches for each month based on different random subsamplings of occurrence data and different random-walk explorations of model solution space using the GARP algorithm. We chose a 'best subset' of these models based on error statistic distributions (Anderson et al., 2003), as follows: a threshold of omission error (failing to predict known presences) was set to 5%, above which models were discarded; among remaining models, median area predicted was calculated; the 10 models with predicted areas closest to the median were identified; and the remaining 10 models were discarded. The geographic predictions (binary predictions, 0=absence, 1=presence) of the remaining 10 models were summed to provide a summary of potential geographic distributions.

Models from a given month were projected onto the landscapes of all succeeding months, thus detecting areas in each future month that fit the ecological requirements of the species as modeled in a particular month. For this implementation, to create the prediction for a given month, we averaged the predictions from the two previous months'

models. Model predictions were evaluated by relating the positions of actual occurrences (vectors or human cases) from the month in question to the predictions from the models in the two preceding months. Chi-square tests were used to compare observed success in predicting the distribution of test points with that expected under a random model (proportional area predicted present provides an estimate of occurrence points correctly predicted were the prediction to be random with respect to the distribution of the test points). As only a single georeferenced human dengue case was available for December 1995, no validations of disease occurrences were carried out for this month.

To establish which environmental dimensions contribute strongly to understanding *Aedes* distributions in space and time, we used the approach outlined by Peterson and Cohoon (1999). Here, for all possible combinations of environmental dimensions, we ran GARP on known occurrences from each month, and measured omission error based on independent subsamples of half the points available for that month. We then calculated Pearson product-moment correlations between inclusion/exclusion of a particular dimension (coded as a binary variable) and the independent omission error measure. Dimensions exhibiting strongly negative correlations are those that contribute to improving models (Peterson and Cohoon, 1999).

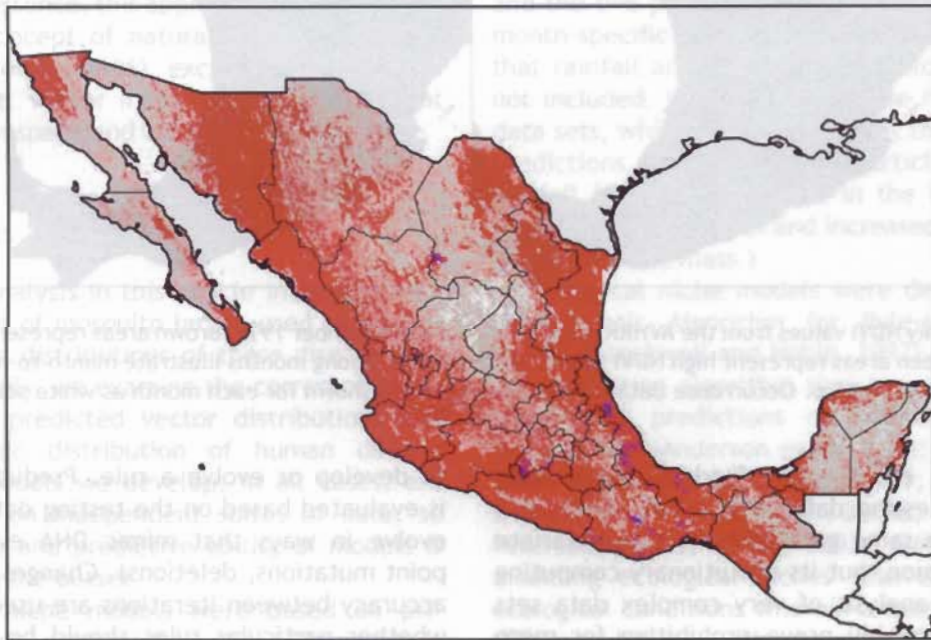


Figure 2 Sampling points (Xs) at which *Aedes aegypti* was encountered, overlain on a prediction of the species' potential distributional area throughout the year, based on annual means of remotely sensed information. White = predicted absent by all models; gray = predicted present by 1–49% of models; pink = predicted present by 50–79% of models; and red = predicted present by >80% of models. Note the broad areas predicted to present conditions within the species' ecological niche over the year.

3. Results

A traditional, time-averaged ecological niche model based on all occurrence points available and conditions averaged over the year indicated a broad potential distribution for *A. aegypti* across

Mexico (Figure 2). This model, however, could not reflect the rather dramatic seasonal shifts in occurrences of the mosquitoes: during the summer occurrences were principally in the southeastern and southern lowlands, whereas during the autumn and early winter months occurrences were farther

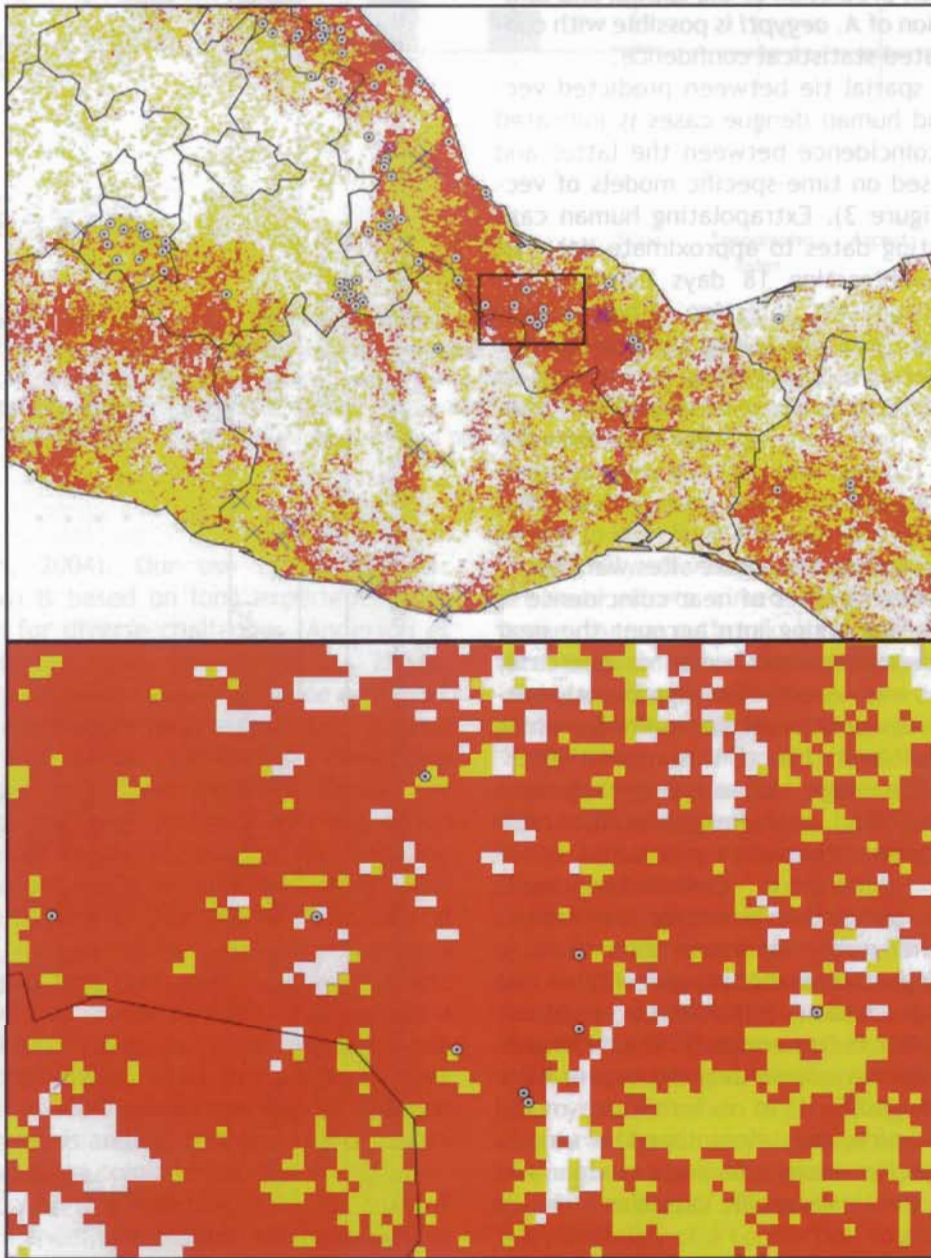


Figure 3 Comparison of time-specific and time-averaged ecological niche models in central and southern Mexico, with a model for August 1995 in yellow (based on areas predicted by the majority of models in the average of the predictions for August from June and July 1995) overlain on the annual mean model shown in Figure 1 (areas in red predicted present by all models). Also shown are occurrences of the vector species in August (blue Xs) and human dengue cases (dotted circles). The top panel shows central and southern Mexico; the bottom panel shows the detail of an area (see inset on top panel) of seeming model failure that, viewed carefully, can be seen to reflect fine-scale coincidence between disease occurrence and time-specific predictions.

north and in the interior of the country. Time-specific models, by contrast, predicted much more restricted areas in any one month (e.g. Figure 3). The small areas predicted in particular months coincided with actual occurrences much better than random models ($P < 0.05$) for all months tested except October 1995 ($P \gg 0.05$) and November 1995 ($0.05 < P < 0.10$; Table 1). Hence, at least for large parts of the year, prediction of the spatial and temporal distribution of *A. aegypti* is possible with considerably elevated statistical confidence.

A potential spatial tie between predicted vector activity and human dengue cases is indicated by excellent coincidence between the latter and predictions based on time-specific models of vector activity (Figure 3). Extrapolating human case serological testing dates to approximate dates of exposure (by subtracting 18 days for infection of mosquito, incubation, infection of human, and incubation, and 7 days for taking sera after onset of symptoms), and overlaying these occurrences on mosquito predictions for those time periods, time-specific models predicted 34% less area than the time-averaged models; and yet they were successful in anticipating 62% of dengue cases, a figure that would improve considerably if actual radii of human movements and possible exposure sites were taken into account (see examples of near-coincidence in Figure 3). Even not taking into account the near misses, coincidence between human dengue cases and predictions was nevertheless significantly better than random models for all six months for which testing was possible (i.e. June–November 1995).

Using the coverage subsampling approach described above and elsewhere (Peterson and Cohoon, 1999), we achieved a picture of which environmental dimensions contributed most strongly to the predictive power of our models (Figure 4). The most important dimension in creating highly predictive models was NDVI in the month of the prediction, followed by elevation, NDVI two months before, and NDVI one month before; slope, topographic index and aspect were statistically insignificant in determining model predictivity. As such, it is clear that the success of our time-specific models depends in clear and direct ways on the time-specific variables included in the models.

4. Discussion

The modeling approach explored in this article represents a first application of ecological niche modeling across both space and time (Soberón

Table 1 Summary of results of predictions of mosquito presences and human dengue cases for particular months in 1995 based on averages of the two previous months' ecological niche model predictions

Time period	Mosquito distributions			Human dengue cases				
	N (test points)	% correct	% of area predicted present (50 km buffer)	P	N (test points)	% correct	% of area predicted present (150 km buffer)	P
Whole year (time-averaged model)	181	95.0	78.5	*	1994	86.6	71.5	*
June	22	72.7	49.6	*	92	70.7	55.0	*
July	28	82.1	59.2	*	195	74.4	55.7	*
August	40	75.0	44.7	*	714	61.5	38.9	*
September	25	80.0	44.6	*	599	78.0	36.7	*
October	19	78.9	66.6	*	356	60.1	49.0	*
November	25	76.0	66.1	+	30	26.7	49.1	*
December	22	95.5	78.6	*	—	—	—	—

* Positive statistical significance of comparison with a random model ($P < 0.05$, in most cases $P \ll 0.05$).

+ Marginal statistical significance of comparison with a random model ($0.05 < P < 0.10$).

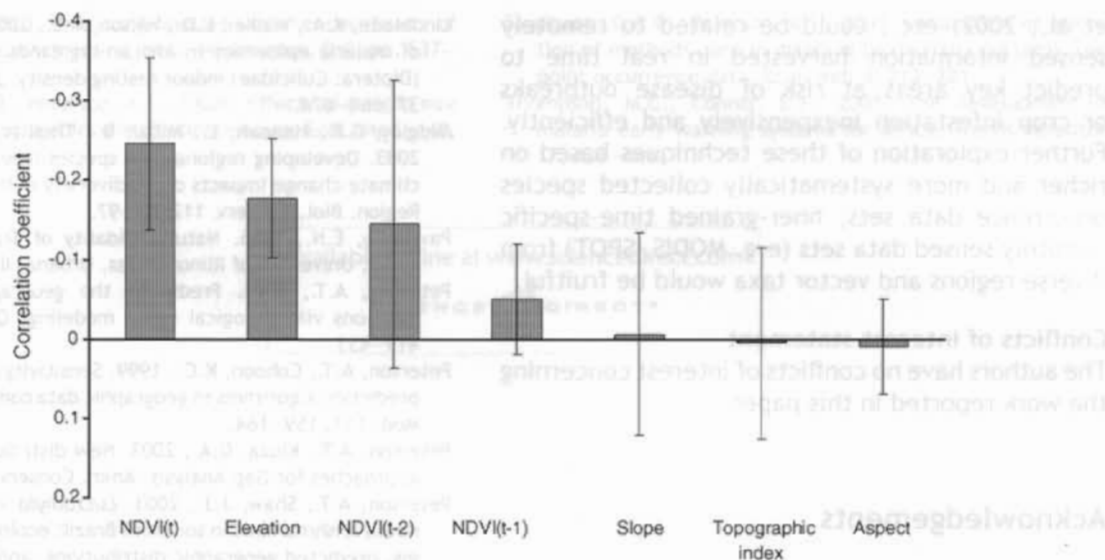


Figure 4 Summary of results of coverage subsampling analyses, indicating relative contributions of each environmental dimension to reducing omission in replicate models. Strongly negative correlations (note that axis is plotted reversed) indicate coverages important in producing low-omission models; error bars indicate the standard deviation in correlation coefficients across months. NDVI (t) is the NDVI value in the month in question; NDVI (t-1) and NDVI (t-2) are the differences between the month in question and one or two month preceding.

and Peterson, 2004). Our use of the genetic algorithm (GA) is based on long experience with this approach for diverse challenges (Anderson et al., 2003; Peterson, 2003; Peterson et al., 2002a, 2004a). Comparisons of GA performance with that of statistical approaches (e.g. multivariate logistic regression) and other evolutionary-computing approaches are in process (National Center for Ecological Analysis and Synthesis working group 'Testing Alternative Methodologies for Modeling Species' Ecological Niches and Predicting Geographic Distributions'), but the GA in general appears very well-suited for analysis of complex environmental spaces, such as that in this project.

The random null model that we have used as a basis for statistical validation of our models is not particularly challenging. What this approach does offer, however, is confirmation that the coincidence between our models and our test occurrence points is not simply random coincidence. The complimentary dimension of this question, then, is that of model performance: our models averaged 80% in predicting mosquito occurrences from two consecutive months to the next, which is quite high, given the complexities of mosquito distributions and the rather sparse nature of the occurrence data on which the models were based.

These results open a new suite of possible applications of remotely sensed information to epidemiology, taking advantage of the excellent

predictivity afforded by ecological niche modeling. Previous efforts aimed at forecasting mosquito-borne disease outbreaks have based predictions on past patterns of epidemics (Abeku et al., 2002), climate anomalies (Thompson and Connor, 2001) or observed vector biting activity (Lindblade et al., 2000). More recently, attempts have been made to use remotely sensed information (Hay et al., 2001, 2003; Rogers et al., 2002), but seeking a direct association between the imagery and human disease outbreaks.

Our work seeks a more process-oriented middle ground: occurrence information for species that are key to the disease transmission cycle is related to remotely sensed data to produce a vector species-specific model; these models are then assembled in a GIS environment to reconstruct disease transmission cycles (Peterson et al., 2002b, 2003). Although clearly we have not yet assembled the full picture of dengue transmission patterns in Mexico, the predictable nature of vector distributions is clear, and the possibility of a connection to disease transmission to humans is suggested.

Time-specific ecological niche modeling has the potential for development into real-time forecast systems for geographic phenomena related to biodiversity. 'Libraries' of ecological niche models for vector and reservoir species in disease cycles, crop pests (Sánchez-Cordero and Martínez-Meyer, 2000) and agricultural species (Báez-González

et al., 2002) etc., could be related to remotely sensed information harvested in real time to predict key areas at risk of disease outbreaks or crop infestation inexpensively and efficiently. Further exploration of these techniques based on richer and more systematically collected species occurrence data sets, finer-grained time-specific remotely sensed data sets (e.g. MODIS, SPOT) from diverse regions and vector taxa would be fruitful.

Conflicts of interest statement

The authors have no conflicts of interest concerning the work reported in this paper.

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