

Potential Distribution of Two Species in the Medically Important *Anopheles minimus* Complex (Diptera: Culicidae)

DESMOND H. FOLEY,^{1,2} LEOPOLDO M. RUEDA,¹ A. TOWNSEND PETERSON,³
AND RICHARD C. WILKERSON¹

J. Med. Entomol. 45(5): 852–860 (2008)

ABSTRACT *Anopheles minimus* Theobald (= *An. minimus* A) and possibly *Anopheles harrisoni* Harbach & Manguin (= *An. minimus* C) are important malaria vector species in the Minimus Complex in Southeast Asia. The distributions of these species are poorly known, although detailed information could benefit malaria vector incrimination and control. We used published collection records of these species and environmental geospatial data to construct consensus ecological niche models (ENM) of each species' potential geographic distribution. The status of the Indian taxon *An. fluviatilis* S as a species distinct from *An. harrisoni* has been debated in the literature, so we tested for differentiation in ecological niche characteristics. The predicted potential distribution of *An. minimus* is more southerly than that of *An. harrisoni*: Southeast Asia is predicted to be more suitable for *An. minimus*, and China and India are predicted more suitable for *An. harrisoni*, so *An. harrisoni* seems to dominate under cooler conditions. The distribution of *An. minimus* is more continuous than that of *An. harrisoni*: disjunction in the potential distribution of the latter is suggested between India and Southeast Asia. *Anopheles fluviatilis* S occurrences are predicted within the *An. harrisoni* ecological potential, so we do not document ecological differentiation that might reject conspecificity. Overall, model predictions offer a synthetic view of the distribution of this species complex across the landscapes of southern and eastern Asia.

KEY WORDS ecological niche, distribution, *Anopheles minimus*, *Anopheles harrisoni*, *Anopheles fluviatilis* S

The paucity of detailed information on the geographic distributions of malaria vector species has been a major limiting factor for global modeling of transmission risk (Rogers and Randolph 2003, Tatem et al. 2006). However, the recent availability of tools for ecological niche modeling (ENM) has made possible development of high-resolution maps for mosquito species (Levine et al. 2004a,b). The ecological niche of a species or population is the set of environmental conditions within which it is able to maintain populations without immigration (Grinnell 1917, Holt and Gaines 1992). Previous ENM applications outlined the ecological niche and potential geography of *An. quadrimaculatus* Say (Levine et al. 2004a), *An. gambiae* Giles (Levine et al. 2004b), *Anopheles farauti* Laveran (Sweeney et al. 2006, 2007), *Aedes albopictus* (Skuse) (Benedict et al. 2007), and a set of 10 anopheline

species in Africa (Moffett et al. 2007). All previous mosquito applications of ENM used the evolutionary computing approaches of genetic algorithms (Stockwell and Noble 1992) and maximum entropy (Phillips et al. 2006), although more diverse options exist (Elith et al. 2006).

Ecological niches are estimated as models based on point-occurrence data as they relate to digital geospatial data layers summarizing environmental variation. Georeferenced mosquito point occurrence data are available from the literature or from museum records; an online database for lodging mosquito collection records and distribution predictions has recently become available through MosquitoMap (www.mosquitomap.org). The availability of distribution models for vector species, hosts and pathogens will enable detailed disease risk mapping based on the predicted co-occurrence of these organisms.

Malaria Vectors of Southeast Asia. For Southeast Asia, three main malaria vector groups are recognized: the Dirus Complex, occurring in forested areas; the Minimus Complex, widespread in hilly forested regions; and the Sundaicus Complex, denizens of brackish water areas along coasts (Garros et al. 2006). Here, we focus on the distribution of the Minimus Complex, species *An. minimus* species A and C. Recently, Harbach et al. (2006) formally defined *An. minimus* A as

This research was performed under a Memorandum of Understanding between the Walter Reed Army Institute of Research and the Smithsonian Institution, with institutional support provided by both organizations. The published material reflects the views of the authors and should not be construed to represent those of the Department of the Army or the Department of Defense.

¹ Department of Entomology, Walter Reed Army Institute of Research, 503 Robert Grant Ave., Silver Spring, MD 20910.

² Corresponding author, e-mail: foleydes@si.edu.

³ Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045.

An. minimus Theobald sensu stricto (hereafter *An. minimus*) and Harbach et al. (2007) named *An. minimus* C as *An. harrisoni* Harbach and Manguin. Differences in phenology between *An. minimus* and *An. harrisoni* have been noted in Thailand and Vietnam (Garros et al. 2006). Vectorial status is uncertain, although *An. minimus* seems to be a more efficient malaria vector than *An. harrisoni* (Trung et al. 2004, Garros et al. 2005b). Using remotely sensed data, Rongnoparut et al. (2005) concluded that *An. minimus* has broader habitat preferences than *An. harrisoni*, and uses denser forest, as opposed to open agricultural fields.

The distribution of the Minimus Complex extends from India (Uttar Pradesh to Andhra Pradesh), across Indochina to the Thailand-Malaysia border, and northward across southern China (Harrison 1980). This species complex may occur to 30° N in India and China, and probably does not occur south of 6° N (Harrison 1980). Chen et al. (2002) reported *An. harrisoni* in southern China up to 32.5° N. Srivastava et al. (2005) concluded that areas of northeastern India are favorable for *An. minimus* sensu lato, after integrating thematic maps of soil, forest cover, rainfall, temperature and altitude in a geographic information system (GIS). The Minimus Complex is made up of *An. minimus* and *An. harrisoni* on the Southeast Asian mainland and *An. minimus* E in the Ryukyu Archipelago of Japan. No comprehensive summary of distribution of each member of the complex is available (Garros et al. 2006).

The Indian taxon *An. fluviatilis* S was regarded as conspecific with *An. harrisoni* by Garros et al. (2005a) based on molecular evidence and similarity in bionomics and malaria transmission data, but this conclusion was disputed by Singh et al. (2006), based on additional molecular sequence differences. If conspecific, the distribution of *An. harrisoni* would extend to northwestern India (Garros et al. 2006). Molecular data suggest that only *An. minimus* occurs in Taiwan (Chen et al. 2002, Somboon et al. 2005) and Assam State, India (Prakash et al. 2006, Singh et al. 2006). *An. minimus* and *An. harrisoni* are known to be sympatric across large areas of southern China, Thailand, northern Vietnam, and northern Laos (Garros et al. 2006, 2008). Evidence of genetic homogeneity of *An. harrisoni* over a broad area (Sharpe et al. 2000) is at odds with the assumption of a patchy or restricted distribution of this species (Garros et al. 2005b, 2006).

The geographic range of the Minimus Complex may be unstable, as it had been recorded from peninsular Malaysia, Nepal, and several parts of India, but has not been recorded from these places recently (Garros et al. 2006). Harrison (1980) speculated that pollution, alteration of stream habitats, and the DDT house-spray malaria control program may have eliminated this taxon from some areas. Jambulingam et al. (2005) reported that *An. minimus* reappeared in the Singbhum Hills of east-central India possibly as a result of scaling back of residual insecticide spraying. Garros et al. (2005b) noted the replacement of *An. minimus* by *An. harrisoni* at a site in central Vietnam after 1998 and

suggested that it resulted from introduction of permethrin-treated bed nets.

Here, our aim is to present ENM-based distributional predictions for *An. minimus* and *An. harrisoni* based on occurrence records derived from the literature. We use ENMs for *An. harrisoni* to provide a new perspective on the hypothesis that this taxon is conspecific with *An. fluviatilis* S. More generally, we present a framework for derivation of a more complete understanding of mosquito species' distributions based on currently available occurrence data.

Materials and Methods

Species Occurrence Data. The occurrence points of *An. minimus* and *An. harrisoni* were drawn from Chen et al. (2002), Garros et al. (2008), Green et al. (1990), Kegne et al. (2001), Kengluocha et al. (2005), Phuc et al. (2003), and Trung et al. (2004). Additional occurrence points came from Van Bortel et al. (1999) and Singh et al. (2006) for *An. minimus* and *An. harrisoni*, respectively. The geocode for Ban Phu Rat in Green et al. (1990) was corrected in Sharpe et al. (1999). The record of *An. harrisoni* from Lang Nhot, Vietnam, by Garros et al. (2005b) was excluded, because populations there are not stable; also, the georeference for Binh Thuan provided by Phuc et al. (2003) lay off the coast so a new georeference for this location (11.1833° N, 108.7000° E) was obtained through the Alexandria Digital Library Gazetteer (<http://www.alexandria.ucsb.edu/gazetteer/>). The resulting data set was made up of 73 unique occurrence sites for *An. minimus* and 42 for *An. harrisoni*. Seven records for *An. fluviatilis* S were obtained from the state of Orissa, India: three from Singh et al. (2006), and four from Mohanty et al. (2007). All occurrence locality data used in this study are available at <http://www.mosquitomap.org/> with the global unique identifiers MMap:LitRev:MMap1-122.

Environmental Data. We obtained GIS raster data layers summarizing elevation and a selection of 30 are second resolution climate layers for 1950-1990 from the WorldClim data set (Hijmans et al. 2005, <http://www.worldclim.org/>). Climate layers included temperature (maximum, minimum, mean), precipitation, and 19 "bioclimatic" layers (representing annual trends, seasonality, and extreme or limiting environmental factors). Temperature and precipitation data were restricted to February, April, June, August, October, and December. We also obtained five layers summarizing aspects of topography and landform (compound topographic index, slope, aspect, flow direction, flow accumulation) from the U.S. Geological Survey's Hydro-1K Elevation Derivative Database (<http://edc.usgs.gov/products/elevation/gtopo30/hydro/>, native resolution 1 by 1 km). The compound topographic index layer summarizes upward curvature of land surface and consequent water pooling, which is important for mosquito development.

We drew further data layers summarizing the photosynthetic capacity or "greenness index" termed the normalized difference vegetation index (NDVI; 0.0091° resolution) (Tucker 1979) from the Advanced Very High

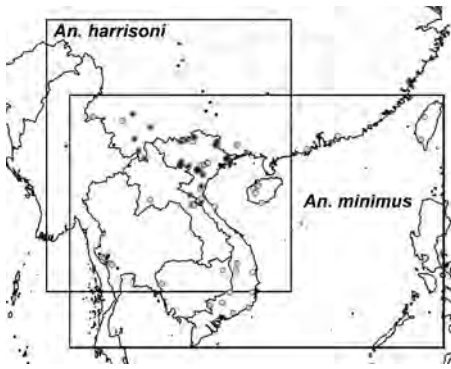


Fig. 1. Location of known occurrences of *An. minimus* (open gray circles) and *An. harrisoni* (smaller closed black circles), with the ecological niche model training area for each species shown.

Resolution Radiometer (AVHRR) satellite (<http://glcf.umiacs.umd.edu/data/landcover/>) for 6 mo in 1992–1993 (February, April, June, August, October, and December). Data layers summarizing percentage of tree cover and 13 classes of land use/land cover (0.0083° resolution) were obtained from the Global Land Cover Facility (<http://glcf.umiacs.umd.edu/data/>). Data on soil taxonomy suborders (0.0333° resolution) were obtained from the U.S. Department of Agriculture National Soils Conservation Service (<http://soils.usda.gov/use/worldsoils/mapindex/order.html>), and data on areas equipped for irrigation (0.0833° resolution) were obtained from the Aquastat site of the Food and Agriculture Organization (<http://www.fao.org/nr/water/aquastat/main/index.stm>); all “no data” cells reclassified to zero irrigation.

All 59 environmental data layers were resampled with bilinear interpolation (Phillips et al. 2006) to a pixel resolution of 0.04°. Layers were clipped to an area encompassing the likely range of *An. minimus* and *An. harrisoni* in Southeast Asia and India (0.10° S–36.78° N, 72.38–122.90° E), for a total of 1.1×10^6 pixels. Because overfitting is more likely in highly dimensional environmental spaces (Peterson et al. 2007a), we used a principal components analysis (PCA based on correlation matrix; in Minitab 15.1.1.0, Minitab Inc., State College, PA) of the full set of 59 environmental layers to create 15 new axes summarizing overall variation in fewer, independent dimensions. The first 15 PCs explained >95% of the overall variation in the 59 original environmental parameters (Peterson 2007). Models for particular species were developed within rectangular subregions surrounding the known occurrences (*An. minimus*, 8.42–25.74° N, 96.42–122.10° E; *An. harrisoni*, 12.22–30.86° N, 94.94–111.66° E; Fig. 1). Models based on these restricted areas were projected onto the broader study region for final analysis and are available at <http://www.mosquitomap.org/>.

Ecological Niche Models. We used the genetic algorithm for rule-set prediction (GARP, Stockwell and Noble 1992) and a maximum entropy approach (Maxent, Phillips et al. 2006) for ENM development. These algorithms were selected because both have been

used in ENM development for mosquitoes (see Introduction), and both have seen intensive analysis of performance (e.g., Peterson et al. 2007a, Phillips 2008).

We used a desktop version of GARP (Desktop GARP 1.1.3, Scachetti-Pereira 2003). GARP uses an iterative process of rule selection, evaluation, testing, and incorporation or rejection. A rule is selected and applied to the training data (half of points input into the program). The genetic algorithm in GARP allows rules to “evolve” to maximize predictive accuracy. The change in predictivity between iterations is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs until convergence (set at 0.01) or to a maximum of 1,000 iterations. We generated 500 models for each species, and selected the 10 “best” models based on omission and commission error statistics (Anderson et al. 2003); specifically, we used an absolute omission threshold of 10% and the central 50% of the commission index distribution.

Maxent has been described and tested in detail previously (Phillips et al. 2006), and we used version 2.2.0 (Phillips 2006). Maxent is based on the idea that the best explanation for unknown phenomena will maximize the entropy of the probability distribution, subject to the constraint of the environmental conditions observed at sites where species have been detected. We used default parameters for Maxent models, except that a random seed was used. Output format was the logistic default option, which can usually be interpreted as relative suitability.

We challenged both GARP and Maxent models to predict into broad areas from which no occurrence data were used in model training by means of “holding back” occurrence data from half of the study area *a priori*. Specifically, we divided the known occurrence points into four quadrants based on their falling above or below the median latitude and above or below the median longitude. Then, we used two quadrants (upper left and lower right, “on-diagonal”) for model development, and the other two (“off-diagonal”) to test model predictions. This methodology has been used for validation in several previous studies (e.g., Peterson and Shaw 2003, Peterson et al. 2007b) and seriously challenges model predictivity by creating broad, unsampled regions for testing. For comparison, we also tested models based on random 50% splits of available occurrence points. In all cases, tests were repeated using reversed training and testing data: first A was used to predict B, then B was used to predict A.

Model Evaluation. Extrinsic test data were overlaid onto predicted distributions and observed correct predictions were tallied. The observed degree of coincidence was tested according to random expectations, calculated as the product of the number of testing points and the proportional coverage of the study area predicted to be present. We followed Anderson et al. (2002) and Peterson et al. (2007b) in using cumulative binomial probabilities that the observed success could be the result of random association between predictions and test points as a test statistic. The more cus-

tomy receiver operating characteristic analysis was not used in this study owing to recent criticisms and concerns about bias and artifact (Lobo et al. 2008, Peterson et al. 2008).

Consensus Predictions. As some studies (e.g., Peterson et al. 2007a) have suggested that Maxent models may be better for interpolation and GARP models better for extrapolation (i.e., transferability), we investigated combinations of the two model outputs. Given concerns expressed by Peterson et al. (2008), in which lower omission model predictions are emphasized, an ideal combined model would predict a smaller area, but would maintain low omission rates. One option for combining models is to consider areas of *intersection*. Unless models are identical, the area of intersection will be smaller, and omission potentially higher, than for either model. Another approach is to *sum* models; summed areas will generally be larger, and omission potentially lower, than for either model, depending on thresholding. Another option for combining models is through a *multiplicative* approach after rescaling the two sets of scores to the same scale: the two (at 0–10) can be multiplied to produce a surface that would range from 0 to 100, with the highest score assigned to pixels that are accorded maximum suitability scores by both GARP and Maxent. Finally, *mosaic* models might combine the area within the boundaries of input occurrence points of the model that is better at interpolation (e.g., Maxent) with the area beyond the boundaries of input occurrence points of the model that is better at extrapolation (e.g., GARP). However, protocols have not been developed for mosaic modeling, so this approach is not considered further here.

To permit visualization of the ecological dimensions of models, we combined the model predictions with the original input environmental grids and exported the associated attributes table in ASCII. We then used Minitab to graph ecological parameters associated with pixels predicted to be present or absent for both species.

Results

The results from the PCA of environmental data revealed that the first principal component (PC1) was most closely related to aspects of temperature, whereas PC 2 and PC 3 were related mainly to precipitation (data not shown). Subsequent PCs emphasized temperature seasonality (PC 4), landcover (PC 5), topography (PC 7–10), NDVI extremes (PC 12, 13), soil (PC 13), precipitation extremes (PC 14), and irrigation (PC 11, 15). In all, the first 15 PCs captured 96.6% of the overall variation in the original 59 environmental data layers.

Coincidence of test occurrence points (two quadrant-based and two random subsets) with predicted areas was very good for *An. harrisoni*, but less so for *An. minimus*. All 40 thresholds (10 per subset) for GARP and 36 of 40 for Maxent were better than random expectations ($P < 0.05$) for *An. harrisoni*. However, for *An. minimus*, only 13 of 40 thresholds in GARP models

and 29 of 40 thresholds in Maxent models were significantly ($P < 0.05$) better than random expectations. Hence, despite smaller sample sizes for *An. harrisoni*, this species was consistently predicted by the models more accurately than *An. minimus*.

Models for *An. minimus* and *An. harrisoni* based on all data points and projected onto the overall area of interest identified broad potential distributional areas across Asia, although differences were apparent between species and algorithms (Figs. 2 and 3). The predicted potential distribution of *An. minimus* is more southerly than that for *An. harrisoni*, particularly noticeable in Southeast Asia, which is predicted to be more suitable for *An. minimus*, and in China and India, which are predicted to be more suitable for *An. harrisoni*. Both modeling approaches coincided with known occurrences of the species, although GARP predictions tended to be more extensive than Maxent predictions, as has been found in other studies (e.g., Peterson et al. 2007a).

Combining GARP and Maxent models by the multiplicative approach resulted in models that more closely resembled Maxent than GARP output (Figs. 2 and 3). Because the distribution of GARP thresholds is skewed toward higher thresholds than those of Maxent (Peterson et al. 2007a, 2008), the impact of GARP output on the resulting distribution of multiplied scores is reduced. We also investigated combining GARP and Maxent models by the intersection and summation method to see whether we could maintain acceptable levels of omission while minimizing geographic area predicted present. An 0.05 omission threshold for *An. minimus* corresponded to an area covered by ≥ 7 best GARP models and to pixels of ≥ 21 suitability for Maxent models. For *An. harrisoni*, the parallel values were ≥ 8 and ≥ 21 , respectively. An 0.15 omission threshold for *An. minimus* corresponded to an area covered by the 10 best GARP models and to pixels of ≥ 41 suitability for Maxent models. For *An. harrisoni*, these values were ≥ 9 and ≥ 41 , respectively.

As anticipated, summing GARP and Maxent models with a threshold at 0.15 omission resulted in a model that approximated the performance of GARP and Maxent models at a lower (0.05) omission threshold (results not shown). However, the best performance seems to be for an intersection of models thresholded at 0.05 omission error. For *An. minimus*, this approach resulted in a similar or smaller area (52.2% of the total area) than was predicted for GARP (69.5%) and Maxent (52.0%) models, while maintaining a low (0.047) omission error. For *An. harrisoni*, this approach resulted in a smaller area (33.2%) than that predicted present by GARP (39.5%) and Maxent (44.0%) models, while maintaining a low (0.043) omission error. The multiplicative and intersection approaches (0.05 omission threshold) for combining the two model results are shown in Figs. 2 and 3.

Seven collection sites for *An. fluviatilis* S from the literature were available to us. For both *An. harrisoni* and *An. minimus*, and under both modeling approaches, these seven points were included within the modeled niche envelope (Figs. 2 and 3): the mean

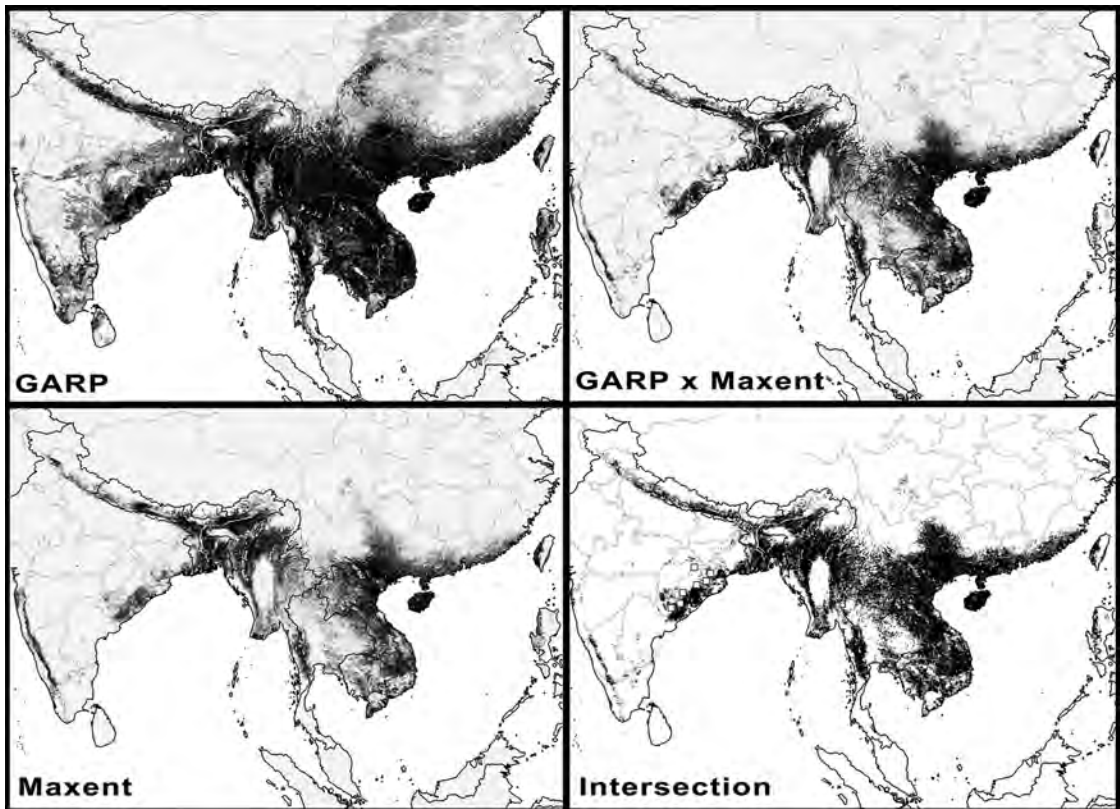


Fig. 2. Predicted distribution of *An. minimus* by using a GARP and a Maxent approach. Consensus distributions by the multiplicative and intersection (thresholded at 0.05 omission error) approaches are also shown. Darker areas indicate greater confidence in predicted presence. Locations shown in India for the intersection model are for *An. fluviatilis* S.

model agreement among the 10 “best” GARP models for these seven sites was 6.1 and 8.7 for *An. minimus* and *An. harrisoni*, respectively; the corresponding mean Maxent suitability scores were 19 and 57, respectively. As such, model projections for *An. harrisoni* may fit somewhat better to these locations than model projections for *An. minimus*.

The two species overlap broadly in ecological space (Fig. 4). However, the niche envelope for *An. minimus* ranges more broadly into hotter and wetter climates, whereas that for *An. harrisoni* includes cooler and drier climates.

Discussion

The distributions developed based on ENMs generally agree well with distributional patterns not included in our analyses, such as in Harrison (1980) for the *An. minimus* complex. Recent ground-truthing of GIS-based predictions for *An. minimus* s.l. in India revealed its reappearance at Banbasa in Uttaranchal, and a first report from Dhubri District (=Dhuburi) in Assam (Srivastava et al. 2005). Our *An. minimus* models indicate environmental suitability in these areas. Singh et al. (2006) documented *An. harrisoni* in central Myanmar, and the ENM results support this observation. Absence data are less informative for assessing

model accuracy because ENM reveals potential distributions rather than actual distributions; other factors such as historical, physical, climatological and biotic constraints may limit distribution (Soberón and Peterson 2005, Peterson 2006a). Thus, the models predict the potential for these species to exist outside the known range, such as in western India, but these species may not have had the chance to disperse and colonize that far. However, a map for *An. minimus* s.l. in Thailand (Harrison 1980, fig. 17) indicated absence of this taxon in southern Thailand and the region north of the Gulf of Thailand, which our models predict absent as well. Chen et al. (2002) reported *An. minimus* s.l. as absent in Chongqing and central northern Guangdong in China; our models show low suitability scores for these regions (Figs. 2 and 3).

The hotter–wetter climate tolerances of *An. minimus* (Fig. 4) mirrors the more southerly extension of this species into tropical regions of Indochina, and the cooler–drier tolerance of *An. harrisoni* concurs with its extension into more temperate areas of China. Because the potential distribution of *An. harrisoni* seems more northerly than that of *An. minimus*, the former species is likely predominant under cooler conditions, such as at higher elevations. Differences in the recorded elevational occurrences of the *An. minimus* complex may reflect differences in the species com-

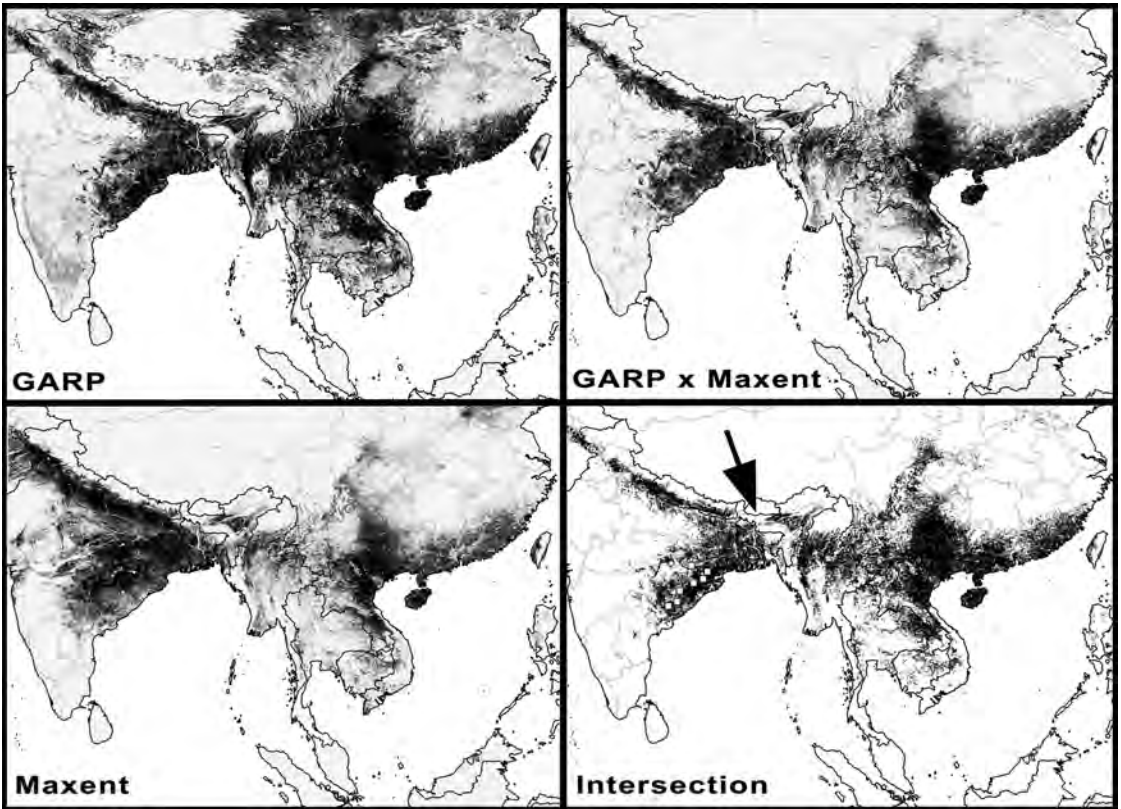


Fig. 3. Predicted distribution of *An. harrisoni* by using a GARP and a Maxent approach. Consensus distributions by the multiplicative and intersection (thresholded at 0.05 omission error) approaches are also shown. Darker areas indicate greater confidence in predicted presence. Arrow indicates location of possible spatial discontinuity. Locations shown in India for the intersection model are for *An. fluviatilis* S.

position in these regions. Harrison (1980) noted that *An. minimus* s.l. immatures were not collected over 672 m in Nepal (Pant et al. 1962), but they were found

up to 1,500 m in Vietnam (Lysenko and Tang-Wang-Ngy 1965). Based on our ENM results and observations in the literature, the Nepalese records probably refer to *An. minimus*, whereas either species is possible for Vietnam.

Our results also indicate that *An. fluviatilis* S may have a closer ecological similarity to *An. harrisoni* than to *An. minimus*. *Anopheles fluviatilis* s.l. occurs at higher elevations than *An. minimus* s.l. in Nepal (up to 1,829 m, Pant et al. 1962).

Raxworthy et al. (2007) argued that ENM can be useful for delimiting species and populations, particularly in detecting recent parapatric speciation. We used ENM predictions to test the hypothesis that *An. fluviatilis* S shares the same ecological niche as *An. harrisoni*. Members of the same species would have the same ecological niche characteristics (Hutchinson 1965), but different species may or may not possess different fundamental niches. Closely related species have been found to have similar ecological niches due to phylogenetic niche conservatism (Peterson et al. 1999, Peterson 2003, Wiens and Graham 2005).

An. harrisoni and *An. fluviatilis* S were considered conspecific by Garros et al. (2005a), but this conclusion was challenged by Singh et al. (2006) based on

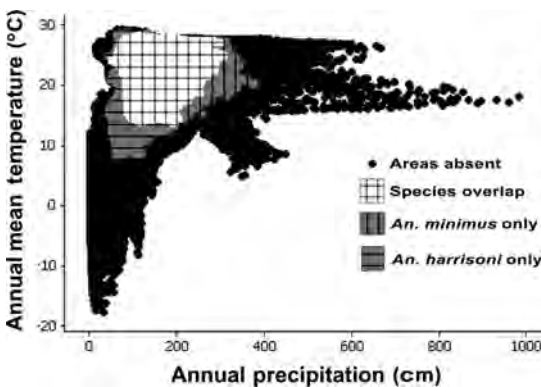


Fig. 4. Distribution of *An. minimus* and *An. harrisoni* in ecological space (annual mean temperature versus annual mean precipitation), based on the intersection of GARP and Maxent models thresholded at 0.05 omission error. The ecological space of each species is shown as vertical or horizontal stripes, the area of overlap between the two species has a hatch pattern, and uninhabited environments are in black.

molecular evidence. Extensive nonoverlap of the ecological niches of these two taxa would be evidence against conspecificity. Ideally, models of ecological niches should be derived for both taxa and the degree of overlap analyzed against null expectations (Stockman et al. 2008). However, collection records for *An. fluviatilis* S are limited so we used the level of omission and probability of occurrence at collection sites of this taxon to assess niche overlap. These comparisons suggested that the two taxa have similar ecological niches, more similar than to *An. minimus*, so our ENM-based analyses cannot reject the null hypothesis that *An. fluviatilis* S and *An. harrisoni* are conspecific.

The distribution of *An. minimus* seems more continuous than that of *An. harrisoni* (Figs. 2 and 3). A likely discontinuity in the distribution of *An. harrisoni* occurs along the eastern border of Bangladesh. The Brahmaputra River seems to constitute a dispersal barrier for gibbons (Takacs et al. 2005), mongoose (Veron et al. 2007), and civet, hog-badger, and Bengal fox (Corbet and Hill 1992). If a barrier exists there that *An. harrisoni* has not been able to breach, other species such as *An. fluviatilis* S may be free from competition to fill its preferred ecological conditions in India. Alternatively, if *An. harrisoni* occurs in India, Indian populations may be genetically differentiated from Southeast Asian populations, given limited gene flow between these regions.

Our distribution models are based largely on yearly climate averages (e.g., WorldClim), and as such are intended to portray general potential distributional tendencies. These predictions are based on presence-only information as well. Improvements in model accuracy could be made by using more sample points, as well as absence information. Levels of precision of location data drawn from the literature are unknown, but the relatively crude spatial resolution at which analyses were conducted (0.04°) makes some error in georeferencing irrelevant.

The realism of ENMs will depend in part on the biological relevance for mosquito biology of the environmental layers. In this study, we use a PCA of 59 environmental data sets as the basis for our analyses, thus including a considerable diversity of environmental information. Nonetheless, more detailed information about irrigation, insecticide usage, insecticide resistance, and extreme weather events may improve predictions. Distribution and abundance of primary malaria vectors may change in response to land-use change, deforestation, pesticide use, and climate change, so the inclusion of more up-to-date information about these phenomena could also improve models. The distribution of *An. minimus* s.l. has changed in the last century, probably due to insecticides used as part of vector control efforts (Harrison 1980, Garros et al. 2005b).

In addition to characterizing distributions of pathogens or vector species, ENM could help us understand the ecology of diseases, identify potential areas for invasion, anticipate the effects of climate change on disease risk, and incriminate unknown vectors or hosts (Peterson 2006b). The known distribution of sibling

species and the collection location of junior synonyms are important information for deciding formal names of members of sibling species complexes that lack diagnostic features and DNA sequence data for type specimens (e.g., Harbach et al. 2007). In cases where extensive mosquito surveys are unavailable from the type locality, models of the potential distribution of mosquito species could play a role in decisions concerning formal naming, especially when synonyms need to be considered.

Acknowledgments

We thank Monica Papeş for advice on analyses. We thank Jean-Paul Chretien for advice and support. Funding for this project was provided by the U.S. Department of Defense Global Emerging Infections Surveillance and Response System, Silver Spring, MD (project G00018_08_WR).

References Cited

- Anderson, R. P., M. Gómez-Laverde, and A. T. Peterson. 2002. Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecol. Biogeogr.* 11: 131–141.
- Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecol. Model.* 162: 211–232.
- Benedict, M. Q., R. S. Levine, W. A. Hawley, and L. P. Lounibos. 2007. Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*. *Vector Borne Zoonotic Dis.* 7: 76–85.
- Chen, B., R. E. Harbach, and R. K. Butlin. 2002. Molecular and morphological studies on the *Anopheles minimus* group of mosquitoes in southern China: taxonomic review, distribution and malaria vector status. *Med. Vet. Entomol.* 16: 253–265.
- Corbet, G. B., and J. E. Hill. 1992. *Mammals of the Indo-Malayan Region*. Oxford University Press, Oxford, United Kingdom.
- Elith, J., C. Graham, R. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettman, J. Leathwick, A. Lehmann, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- Garros, C., R. E. Harbach, and S. Manguin. 2005a. Morphological assessment and molecular phylogenetics of the *Funestus* and *Minimus* Groups of *Anopheles* (*Cellia*). *J. Med. Entomol.* 42: 522–536.
- Garros, C., R. P. Marchand, N. T. Quang, N. S. Hai, and S. Manguin. 2005b. First record of *Anopheles minimus* C and significant decrease of *An. minimus* A in central Vietnam. *J. Am. Mosq. Control Assoc.* 21: 139–143.
- Garros, C., W. VanBortel, Ho Di Trung, M. Coosemans, and S. Manguin. 2006. Review of the *Anopheles minimus* complex of *Anopheles*, main malaria vector in Southeast Asia: from taxonomic issues to vector control strategies. *Trop. Med. Int. Health* 11: 102–114.
- Garros, C., C. Van Nguyen, Ho Di Trung, W. VanBortel, M. Coosemans, and S. Manguin. 2008. Distribution of *Anopheles* in Vietnam, with particular attention to malaria vectors of the *Anopheles minimus* complex. *Malar. J.* 7: 11.
- Green, C. A., R. F. Gass, L. E. Munstermann, and V. Baimai. 1990. Population genetic evidence for two species in *Anopheles minimus* in Thailand. *Med. Vet. Entomol.* 4: 25–34.

- Grinnell, J. 1917. The niche-relationships of the California Thrasher. *Auk* 34: 427–433.
- Harbach, R. E., E. Parkin, B. Chen, and R. K. Butlin. 2006. *Anopheles (Cellia) minimus* Theobald (Diptera: Culicidae) neotype designation, characterization, and systematics. *Proc. Entomol. Soc. Wash.* 108: 198–209.
- Harbach, R. E., C. Garros, N. Duc Manh, and S. Manguin. 2007. Formal taxonomy of species C of the *Anopheles minimus* sibling species complex (Diptera: Culicidae). *Zootaxa* 1654: 41–54.
- Harrison, B. A. 1980. Medical entomology studies XIII. The *Myzomyia* series of *Anopheles (Cellia)* in Thailand, with emphasis on intraspecific variations (Diptera: Culicidae). *Contr. Am. Entomol. Inst.* 17: 1–195.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25: 1965–1978.
- Holt, R. D., and M. S. Gaines. 1992. The analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.* 6: 433–447.
- Hutchinson, G. E. 1965. The niche: an abstractly inhabited hypervolume, pp. 26–78. *In* The ecological theatre and the evolutionary play. Yale University Press, New Haven, CT.
- Jambulingam, P., S. S. Sahu, and A. Manonmani. 2005. Reappearance of *Anopheles minimus* in Singhbhum hills of East-Central India. *Acta Trop.* 96: 31–35.
- Kegne, P., H. D. Trung, V. Baimai, M. Coosemans, and S. Manguin. 2001. A multiplex PCR-based method derived from random amplified polymorphic DNA (RAPD) markers for the identification of species of the *Anopheles minimus* group in Southeast Asia. *Insect Mol. Biol.* 10: 427–435.
- Kengluetcha, A., P. Rongnoparut, S. Boonsuepsakul, R. Sithiprasasna, P. Rodpradit, and V. Baimai. 2005. Geographical distribution of *Anopheles minimus* species A and C in western Thailand. *J. Vector Ecol.* 30: 225–230.
- Levine, R. S., A. T. Peterson, and M. Q. Benedict. 2004a. Distribution of members of *Anopheles quadrimaculatus* Say s.l. (Diptera: Culicidae) and implications for their roles in malaria transmission in the United States. *J. Med. Entomol.* 41: 607–613.
- Levine, R. S., A. T. Peterson, and M. Q. Benedict. 2004b. Geographic and ecologic distributions of the *Anopheles gambiae* complex predicted using a genetic algorithm. *Am. J. Trop. Med. Hyg.* 70: 105–109.
- Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecol. Biogeogr.* 17: 145–151.
- Lysenko, A., and Y. Dang Van Ngi. 1965. Studies on the epidemiology of malaria in North Vietnam. 4. Division of North Vietnam into malariological zones. *Med. Parazit. Parazit. Bolezn.* 34: 189–194.
- Moffett, A., N. Shackelford, and S. Sarkar. 2007. Malaria in Africa: vector species' niche models and relative risk maps. *PLoS ONE* 2: e824. (doi:10.1371/journal.pone.0000824).
- Mohanty, A., P. Kar, K. Mishra, D. V. Singh, N. Mohapatra, S. K. Kar, A. P. Dash, and R. K. Hazra. 2007. Multiplex PCR assay for the detection of *Anopheles fluviatilis* species complex, human host preference, and *Plasmodium falciparum* sporozoite presence, using a unique mosquito processing method. *Am. J. Trop. Med. Hyg.* 76: 837–843.
- Pant, C. P., G. D. Pradhan, Y. Shogaki, and S. L. Shrestha. 1962. Distribution of anophelines in relation to altitude in Nepal. WHO/MAL/343. World Health Organization, Geneva, Switzerland.
- Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* 78: 419–433.
- Peterson, A. T. 2006a. Uses and requirements of ecological niche models and related distributional models. *Biodivers. Inf.* 3: 59–72.
- Peterson, A. T. 2006b. Ecologic niche modeling and spatial patterns of disease transmission. *Emerg. Infect. Dis.* 12: 1822–1826.
- Peterson, A. T. 2007. Why not WhyWhere: the need for more complex models of simpler environmental spaces. *Ecol. Model.* 203: 527–530.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science (Wash., D.C.)* 285: 1265–1267.
- Peterson, A. T., and J. Shaw. 2003. *Lutzomyia* vectors for cutaneous leishmaniasis in Southern Brazil: ecological niche models, predicted geographic distributions, and climate change effects. *Int. J. Parasitol.* 33: 919–931.
- Peterson, A. T., M. Papeş, and M. Eaton. 2007a. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* 30: 550–560.
- Peterson, A. T., R. Williams, and G. Chen. 2007b. Modeled global invasive potential of Asian gypsy moths, *Lymantria dispar*. *Entomol. Exp. Appl.* 125: 39–44.
- Peterson, T., M. Papeş, and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modelling. *Ecol. Model.* (doi:10.1016/j.ecolmodel.2007.11.008).
- Phuc, H. K., A. J. Ball, L. Son, N. V. Hanh, N. D. Tu, N. G. Lien, A. Verardi, and H. Townson. 2003. Multiplex PCR assay for malaria vector *Anopheles minimus* and four related species in the *Myzomyia* Series from Southeast Asia. *Med. Vet. Entomol.* 17: 423–428.
- Phillips, S. J. 2006. Maxent software for species habitat modeling ver. 2.2.0. (<http://www.cs.princeton.edu/~shapire/maxent/>).
- Phillips, S. J. 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). *Ecography* 31: 272–278.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190: 231–259.
- Prakash, A., C. Walton, D. R. Bhattacharyya, S. O'Loughlin, P. D. Mohapatra, and J. Mahanta. 2006. Molecular characterization and species identification of the *Anopheles dirus* and *An. minimus* complexes in north-east India using r-DNA ITS-2. *Acta Trop.* 100: 156–161.
- Raxworthy, C. J., C. M. Ingram, N. Rabibisoa, and R. G. Pearson. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Syst. Biol.* 56: 907–923.
- Rogers, D. J., and S. E. Randolph. 2003. Studying the global distribution of infectious diseases using GIS and RS. *Nat. Rev. Microbiol.* 1: 231–237.
- Rongnoparut, P., D. M. Usgang, V. Baimai, K. Honda, and R. Sithiprasasna. 2005. Use of a remote sensing-based geographic information system in the characterizing spatial patterns for *Anopheles minimus* A and C breeding habitats in western Thailand. *Southeast Asian J. Trop. Med. Public Health* 36: 1145–1152.
- Scachetti-Pereira, R. 2003. DesktopGarp. (<http://www.lifemapper.org/desktopgarp/>).
- Sharpe, R. G., M. M. Hims, R. E. Harbach, and R. K. Butlin. 1999. PCR-based methods for identification of species of the *Anopheles minimus* group: allele-specific amplifica-

- tion and single-strand conformation polymorphism. *Med. Vet. Entomol.* 13: 265–273.
- Sharpe, R. G., R. E. Harbach, and R. K. Butlin. 2000. Molecular variation and phylogeny of members of the *Minimus* group of *Anopheles* subgenus *Cellia* (Diptera: Culicidae). *Syst. Entomol.* 25: 263–272.
- Singh, O. P., C. Chandra, N. Nanda, S. K. Sharma, Pe Than Htun, T. Adak, S. K. Subbarao, and A. P. Dash. 2006. On the conspecificity of *Anopheles fluviatilis* species S with *Anopheles minimus* C. *J. Biosci.* 31: 671–677.
- Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Inf.* 2: 1–10.
- Somboon, P., C. Thongwat, P. Somvang, H. J. Teng, Y. Tsuda, and M. Takagi. 2005. The specific status of *Anopheles minimus* s.l. collected from Taiwan. *Southeast Asian J. Trop. Med. Public Health* 36: 605–608.
- Srivastava, A., B. N. Nagpal, R. Saxena, V. Dev, and S. K. Subbarao. 2005. Prediction of *Anopheles minimus* habitat in India – a tool for malaria management. *Int. J. Geogr. Inf. Sci.* 19: 91–97.
- Stockman, A. K., R. M. Danell, and J. E. Bond. 2008. D-NOVL: a program to simulate overlap between two niche-based distribution models. *Mol. Ecol. Resour.* 8: 290–294.
- Stockwell, D.R.B., and I. R. Noble. 1992. Induction of sets of rules from animal distribution data: a robust and informative method of analysis. *Math. Comput. Sim.* 33: 385–390.
- Sweeney, A. W., N. W. Beebe, R. D. Cooper, J. T. Bauer, and A. T. Peterson. 2006. Environmental factors associated with distribution and range limits of malaria vector *Anopheles farauti* in Australia. *J. Med. Entomol.* 43: 1068–1075.
- Sweeney, A. W., N. W. Beebe, and R. D. Cooper. 2007. Analysis of environmental factors influencing the range of anopheline mosquitoes in northern Australia using a genetic algorithm and data mining methods. *Ecol. Model.* 203: 375–386.
- Takacs, Z., J. C. Morales, T. Geissmann, and D. J. Melnick. 2005. A complete species-level phylogeny of the Hylobatidae based on mitochondrial ND3-ND4 gene sequences. *Mol. Phylogenet. Evol.* 36: 456–467.
- Tatem, A. J., S. I. Hay, and D. J. Rogers. 2006. Global traffic and disease vector dispersal. *Proc. Natl. Acad. Sci. U.S.A.* 103: 6242–6247.
- Trung, H. D., W. VanBortel, T. Sochantha, K. Keokenchanh, N. T. Quang, L. D. Cong, and M. Coosemans. 2004. Malaria transmission and major malaria vectors in different geographical areas of Southeast Asia. *Trop. Med. Int. Health* 9: 230–237.
- Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens. Environ.* 8: 127–150.
- Van Bortel, W., H. D. Trung, N. D. Manh, P. Roelants, P. Verle, and M. Coosemans. 1999. Identification of two species within the *Anopheles minimus* complex in northern Vietnam and their behavioural divergences. *Trop. Med. Int. Health* 4: 257–265.
- Veron, G., M-L. Patou, G. Pothet, D. Simberloff, and A. P. Jennings. 2007. Systematic status and biogeography of the Javan and small Indian mongooses (Herpestidae, Carnivora). *Zool. Scr.* 36: 1–10.
- Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol., Evol. Syst.* 36: 519–539.

Received 21 February 2008; accepted 6 June 2008.