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 Lavern (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...
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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 bio-nomics 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 Singh-bum 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. (2005), Green et al. (1990), Keegne et al. (2001), Kengluecha 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 geocode for Binh Thuan provided by Phuc et al. (2003) lay off the coast so a new geocode 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 MMpLitRev: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; 0.0001” resolution) (Tucker 1979) from the Advanced Very High
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—36.79° N, 72.38—122.90° E), for a total of 1.1 × 10^6 pixels. Because overfitting is more likely in higher 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 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-

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**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.**
tomary 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 $\geq$7 best GARP models and to pixels of $\geq$21 suitability for Maxent models. For An. harrisoni, the parallel values were $\geq$8 and $\geq$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 $\geq$41 suitability for Maxent models. For An. harrisoni, these values were $\geq$9 and $\geq$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
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 suitabilities 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-
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
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 1950, 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.

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