A GLOBAL INDEX REPRESENTING THE STABILITY OF MALARIA TRANSMISSION

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Abstract. To relate stability of malaria transmission to biologic characteristics of vector mosquitoes throughout the world, we derived an index representing the contribution of regionally dominant vector mosquitoes to the force of transmission. This construct incorporated published estimates describing the proportion of blood meals taken from human hosts, daily survival of the vector, and duration of the transmission season and of extrinsic incubation. The result of the calculation was displayed globally on a 0.5° grid. We found that these biologic characteristics of diverse vector mosquitoes interact with climate to explain much of the regional variation in the intensity of transmission. Due to the superior capacity of many tropical mosquitoes as vectors of malaria, particularly those in sub-Saharan Africa, antimalaria interventions conducted in the tropics face greater challenges than were faced by formerly endemic nations in more temperate climes.

INTRODUCTION

Maps representing the world-wide burden of malaria[1] generally reflect the reported distribution of clinical episodes of this disease. However, the scope and accuracy of these reports are limited by the extent of health care coverage, the efficacy of surveillance and reporting systems, and other factors that have little to do with the underlying force of malaria transmission. Schemes using the mortality rates of garrisoned British troops in the early 18th century offer novel insights into the global distribution and variation of malaria risk,[2–4] but represent the experience of an archaic and geographically limited population subject to peculiar behavioral constraints. The underlying force of malaria transmission is better represented by maps representing the climatic determinants of malaria, such as the schemes developed by the "Mapping Malaria Risk in Africa" (MARA) collaboration, are less affected by institutional limitations and are based on more objective ecologic bases.[5] Such maps derive from a "climatic suitability index" that represents the climatic limits on vector distribution and parasite development as well as the presence of a sufficiently long breeding period for the vector population. These variables relate well to depictions in clinically based maps, but do not consider all of the factors intrinsic to vector mosquitoes that affect transmission intensity at a given level of abundance. Temperature, for example, is used only to define the limits and relative suitability of the region as a transmission site. Other maps attempt to bridge these clinically and environmentally based approaches on a regional scale by considering statistical correlations between malaria incidence and environmental characteristics.[6] Such representations of malaria risk improve the resolution of spatial depictions of transmission intensity, but do not consider directly the properties intrinsic to vector mosquitoes that contribute most powerfully to vectorial capacity, such as focused feeding behavior and longevity. Available maps depicting the relative intensity of malaria transmission generally are constructed from surrogates or filtered outcomes that remain one or more steps removed from the forces that govern the stability of malaria transmission.

Malaria is said to be stable if it is transmitted throughout the year by long-lived, anthropophilic vector anopheline mosquitoes. In his seminal 1952 malariologic analysis, Macdonald used a/μ to represent an index of stability based on the two most important components of his vectorial capacity equation,[7] in which a represents the human-biting tendency of the vector and μ the daily mortality rate. Although this index is useful when applied within a given site or between climatically similar sites, it does not account for ambient temperature, which profoundly affects the duration of extrinsic incubation. Although vector longevity contributes to the force of transmission as an exponent of this incubation period, Macdonald's stability convention equates longevity with blood-feeding preference, which participates only as a squared term because at least two feedings are required to complete one transmission cycle. Perpetual transmission is particularly important in the case of malaria caused by *Plasmodium falciparum* because infected people tend to become noninfectious for mosquitoes within two months after they had been infected.[8] These characteristics of stable transmission of malaria can provide a solid foundation for understanding variations in malaria transmission intensity. However, we lack a synthesis of the various designated components of transmission stability that can be used to compare the resiliency of malaria transmission in different sites.

It may be that a global depiction of the intrinsic contribution of mosquito vectors to malaria transmission would provide an objective measure of regional differences in the force of transmission, uncolored by clinical externalities. To depict these relationships, we derived a spatial index of the stability of malaria transmission based on the most powerful intrinsic properties of anopheline mosquito vectors of malaria that interact with climate to determine vectorial capacity. Because this index examines potential transmission stability, it includes regions where malaria is not currently transmitted, but where it had been transmitted in the past or where it might be transmitted in the future. This index, therefore, includes "anophelism (with as well as) without malaria."

MATERIALS AND METHODS

Distribution and characteristics of vectors. The peer-reviewed scientific literature served as the main source of information for characterizing the distribution and for describing certain biologic characteristics of selected anopheline vectors of malaria (Table 1). Although information from primary sources was preferred, more general reviews and texts were consulted. From these sources, we designated the dominant vectors in each of the countries in which malaria is or

TABLE 1
Sources of information on anopheline distribution and seasonality

Region	References
General	1, 9–11
Africa	12–23
South and Central America	8, 24–53
Middle East	54–71
Southeast Asia	72–79
Northern Asia	80–86
Western Asia	87–90
Australasia	91–95
Europe	96–103
North America	104

has been endemic. Only the smallest island nations and protectorates were excluded from these analyses. The level of resolution used also precluded detailed consideration of individual cities. A regionally "dominant" vector was defined as an anopheline that is demonstrably vector competent, frequently contains sporozoites, tends to feed on human hosts, and is more abundant than other anophelines. These considerations were applied independently to each month of the year to permit "swapping" of dominant vectors between seasons within a region. Regions were subdivided when appropriate to permit more than one malaria vector in a country to be designated as dominant.

To describe the seasonal distributions of each regionally dominant malaria vector for each of the 12 months of the year, we determined whether such a mosquito was locally active, using the same body of literature that was used to estimate vector bionomics. Sources of information were favored in which mosquito abundance was monitored systematically by means of landing counts, resting counts, light traps, flit catches, or other such objective methods. Certain of these sources described seasonal abundance in weekly, biweekly, or monthly observations. When no entomologic information was available, we relied on the recorded seasonality of malaria incidence. We consulted as many such reports as could be found and assigned values based on a "majority" of the available records. When no reliable information was available for a site, records of the local climate were interpolated to indicate whether a particular vector may be present there in a given month. The algorithm for decision-making in such anomalous cases varied according to the vector species. For those vectors that breed mainly in temporary water, we used a minimum precipitation threshold of 10 mm per month, lagged one month, to judge when the vector would be present in the site during a given month. Vectors that mainly exploited permanent or semi-permanent bodies of water were considered to be independent of seasonal fluctuations in rainfall unless empirical evidence indicated otherwise. In temperate or altitudinous regions, we used temperature thresholds to determine whether vectors would be active in a particular month, assuming that anophelines remain inactive when the mean monthly temperature remains below 15°C.

Mapping methods. A map of vector distributions was created using ArcView version 3.2[105] geographic information system software. An outline map of political borders was color-coded according to the dominant vector indicated by the literature review. In many cases, countries were divided into one or more subregions to account for ecologic hetero-

geneity in anopheline distribution. Gaps and discrepancies in the resulting preliminary map were corrected according to features of the habitat and climate. Satellite-derived vegetation indices, as indicated by the Global Ecosystem classification of the Global Land Cover Characteristics 1 km Database,[106] provided a means for defining ranges by identifying areas with habitats suitable for vectors with such unique ecologic constraints as salt marshes or forests. The northern limit of the Sahel, for example, was generally defined by the extent of "hot and mild grasses and shrubs." A digital elevation model[107] was used to further define the ranges of vector species that were affected by maximum and, in some cases, minimum altitudinal limits, as reported in the World Malaria Risk Chart.[108] Regions with more than 1.5 days of seasonal frost in the summer[109] served to define the limits of distribution of vectors in the northern latitudes. Maps representing the extrinsic incubation period of *P. falciparum* were based on the 1901–1990 mean monthly temperature records of the International Panel on Climate Change.[109] Human population data were derived from the detailed Gridded Population of the World data set.[110] Data calculated for each month are represented in 0.5° cells.

Our analysis of the distribution of dominant vectors of malaria, therefore, was species specific and based on published reports of anopheline bionomics, vegetation maps (defining suitable, unsuitable habitat), altitude (maxima or minima), monthly precipitation thresholds (minima), and monthly temperature thresholds (minima, isotherms, length of frost-free season).

RESULTS

Selection of regionally dominant vector *Anopheles.* We first identified the countries in which malaria is endemic or has been endemic and enumerated the vector *Anopheles* endemic to the site. Certain of these countries were divided into as many as four regions to represent the diversity of habitats there. To characterize the dominant vector in each region, we selected those that were longest lived and that fed most frequently on human hosts (Table 1). Dominant malaria vectors were designated in each endemic or potentially endemic region (Figure 1). The 260 regions that we identified are infested by a total of 34 dominant vector *Anopheles*.

Derivation of a vector stability index. To depict the relative stability of malaria transmission for each of these potentially malaria-endemic regions, we derived an index that expressed those factors that most powerfully and perennially influence the intensity of malaria transmission. We used, therefore, a subset of the vectorial capacity equation without terms for mosquito abundance or vector competence. We did not consider a recovery rate for infected people. To calculate the duration of the extrinsic incubation period "E," the index (1) was calculated for each month, and biting activity was designated based on the average monthly temperature and Moshkovsky's degree-day-based formulae[111] (2,3).

$$\sum_{m=1}^{12} a_{i,m}^2 \, p_{i,m}^E \Big/ -\ln(p_{i,m})$$

where m = month (1–12), i = identity of dominant vector, a = proportion biting people (0–1), p = daily survival rate (0–1), and E = length of extrinsic incubation period in days
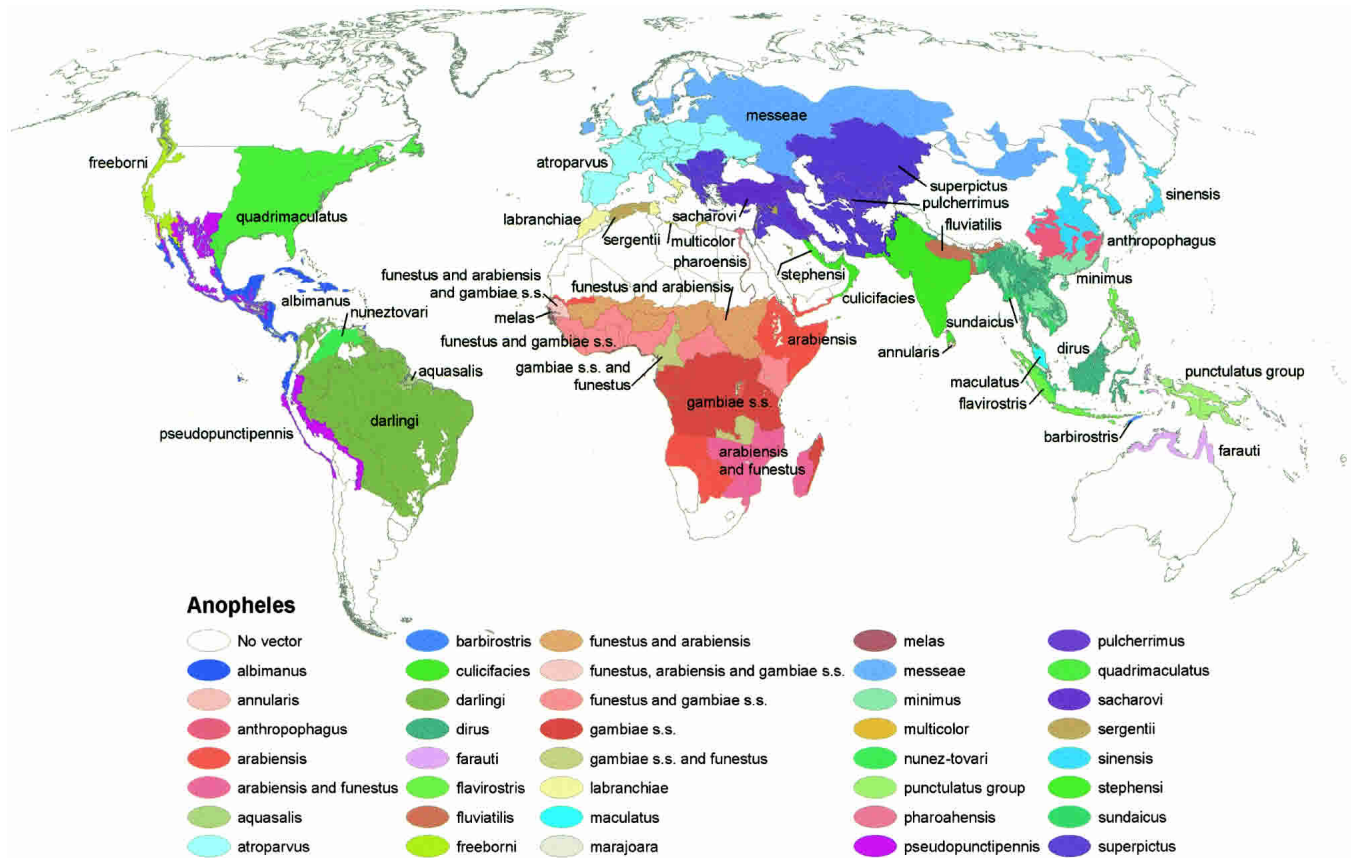
FIGURE 1.   Global distribution (Robinson projection) of dominant or potentially important malaria vectors.

where $E = 111/T\text{-}16$ for *P. falciparum* and $E = 105/T\text{-}14.5$ for *P. vivax*.

Parameterization of the stability index. We first applied our vector stability index to each of the regions designated as infested by one or another of the 34 *Anopheles* vectors that we considered to be dominant. Criteria used to estimate a included field-derived estimates of the human biting index (hbi) based on mosquitoes captured in various locations and whose blood meals were identified by precipitin,[112–117] enzyme-linked immunosorbent assay,[118,119] or gel diffusion methods.[120] Data were excluded if they derived from contrived experiments in which human or other hosts were exposed in a common space. In the case of mixed blood meals, any mosquito yielding evidence of ingested human blood was considered to be a human feeder in the calculation of a. Criteria for estimating daily survival rate (p) in the peer-reviewed literature variously used mark-release recapture tracking of the daily rate of decrease in recaptures,[115,121] the ratio of Stage IV to Stage III ovarioles in dissected adults,[122] the rate of increase in infection rate, parous rates, and directly observed mortality in mosquitoes maintained in cages in the laboratory. A common value for a was assigned to each vector species throughout its range. Where the members of a species complex were sympatric and not readily distinguished by habitat (e.g., *Anopheles punculatus* s.l.), a combined median estimate was used for all members of the taxon. In certain other cases (e.g., *An. fluviatilis* s.l.), in which the habitat preference of the anthropophilic members of the complex (sibling species S) differ from those that are zoophilic (T), the indi-

vidual members were differentiated. Observations made before species complexes were recognized or before these species could readily be distinguished were excluded unless current information on geography or habitat facilitated such a distinction. This criterion excluded many older observations from parts of Africa where *An. arabiensis* and *An. gambiae* are sympatric and share in malaria transmission. The median hbi value for all 34 vectors was 0.672, ranging from 0.01 to 0.98 (Table 2). These values representing a are varied, but consistent.

Survival estimates for adult anophelines were highly variable between studies. The median daily survival value was 0.846, ranging from 0.682 for *An. albimanus* to 0.966 for *An. atroparvus* and *An. quadrimaculatus* (Table 3). Because survival was so infrequently estimated and because the methods of estimation have such disparate biases (e.g., lower mortality from population cages and higher mortality from mark-recapture), the median value of p was applied to all species across their ranges. A coherent value representing the stability index can thus be applied to each dominant vector anopheline.

Adaptation of the stability index to a fine geographic scale. We then depicted our stability index on a geographic scale finer than that represented by the 260 regions that we designated as malarious or potentially malarious. Toward this end, depictions of seasonality in malaria transmission were refined by applying a 10-mm monthly precipitation threshold with a one-month lag that determined whether index values were calculated for individual 0.5° cells. Temperature data

TABLE 2
Human blood index of each of the regionally dominant anopheline vector mosquitoes

Anopheles species	Median human blood index	No. of observations	References
albimanus	0.102	16	123–129
anthropophagus	0.010	1	130
aquasalis	0.109	3	131–132, 249, 250
arabiensis	0.871	32	13, 20, 125, 133–150
atroparvus	0.245	8	151–154, 251
barbirostris	0.127	9	124, 125, 129, 155–158
culicifacies	0.052	55	125, 155, 159–172
darlingi	0.458	2	129, 173
dirus	0.355	18	124, 125, 174–176
farauti	0.658	19	124, 125, 129, 174, 177
flavirostris	0.300	9	125, 129, 174, 176
fluviatilis	0.034	27	58, 124, 125, 129, 155, 167, 169, 178–182
freeborni	0.019	8	104, 183, 184
funestus	0.980	30	12, 118, 125, 138, 139, 143, 185–189
gambiae ss	0.939	36	12, 13, 14, 133, 135, 138, 139, 142, 145, 146, 148, 149, 150, 185, 186, 190–192
labranchiae	0.151	17	103, 123, 124, 128, 193–195
maculatus	0.155	10	125, 155, 156, 158, 196–198
melas	0.690	6	23, 74, 133, 190
messeae	0.172	14	117, 154, 199, 200, 201–204
minimus	0.425	12	125, 151, 176, 197, 205–208
multicolor	0.008	15	62, 124, 125, 209–212
nuneztovari	0.222	11	30, 46, 49, 50, 213, 214
pharoahensis	0.520	17	124, 125, 129, 209, 211, 215–220
pseudopunctipennis	0.477	13	124, 126, 129, 221–223
pulcherrimus	0.062	12	124, 125, 129, 224–227
punctulatus sl	0.855	7	124, 125, 129, 174, 177
quadrimaculatus	0.111	27	228–230
sacharovi	0.087	47	125, 199, 231–241
sergentii	0.100	18	124, 125, 129, 210, 212
sinensis	0.018	21	124, 129, 151, 157, 158, 174, 206, 242–245
stephensi	0.023	37	63, 124, 125, 129, 155, 160, 166, 169, 170, 176, 246
superpictus	0.093	18	59, 124, 129, 193, 199, 231, 234, 240
sundaicus	0.611	17	124, 125, 129, 158, 247–248

were applied on a similar scale to non-zero cells when calculating cell-level indices. The resulting cell-based index characterized broad regions and countries much as did the simpler region-based index while providing less abrupt transitions on the fringes of vector distributions, especially in arid zones. This inclusion of a micro-climate parameter in our index better balances the influence of temperature with that of rainfall, an effect that is more implicit than explicit in the region-based indices. The adjusted monthly maps were combined to create a final map of the malaria stability index (Figure 2). The resulting map resembles other depictions of the intensity of malaria risk throughout the world.[1]

DISCUSSION

Regional differences in stability. Both the region-based and cell-based versions of our stability index demonstrate that malaria is transmitted far more robustly in sub-Saharan Africa than it is elsewhere in the world. In the savannah regions of west and central Africa that border the Sahel, stability is enhanced by the continuous heat that characterizes the region, the human-biting habit of the autochthonous vector mosquitoes and the presence of a complementary vector (*An. funestus*) that maintains transmission during the dry season when the density of the wet-season vectors (*An. gambiae* s.l.) wanes. Transmission is somewhat less stable in Papua New Guinea, Irian Jaya, and the Solomon Islands where particular members of the *An. punctulatus* complex are almost exclu-

sively anthropophilic but where transmission virtually ceases during the rainy season. Malaria is less stable elsewhere in the tropics and least stable in the more temperate parts of the world. Tropical regions in general appear to face larger obstacles in intervening against malaria, which these indices suggest may be due more to the intrinsic properties of their vectors and the effects of climate than to differences in health systems or anti-malaria interventions. These indices also demonstrate the advantages that once were enjoyed in temperate nations that happened not to be burdened by anthropophilic mosquitoes.

Sources of error and bias. The diverse methods that have been used to estimate mosquito survival tend to bias comprehensive longevity estimates. Mark-release recapture methods appear to be most conservative, possibly because mosquitoes are damaged when they are captured and held prior to release. Estimates derived from laboratory-reared mosquitoes, held in population cages, tend to exceed those derived in other ways, reflecting perhaps the absence of such natural hazards as predators. These biases are most apparent in the case of vectors that are represented poorly in the literature. The disproportionate effect of vector longevity on the index further exacerbates the effect of such aberrations. The results of the version of our index based on feeding habit alone are more consistent with clinical experience[1] than is the index that includes both longevity and human-biting habit. The anomaly introduced by the longevity parameter appears to derive more from measurement error, sample size, and incon-

TABLE 3
Survival rate of each of the regionally dominant anopheline vector misquitoes

Anopheles	Median daily survival rate	No. of observations	References
albimanus	0.682	16	128, 252–254
anthropophagus	0.803	1	130
aquasalis	0.776	3	131, 255, 256
arabiesis	0.790	32	143, 144, 149, 257
atroparvus	0.966	8	258–262
barbirostris	0.980	9	157
culicifacies	0.831	55	69, 166, 170, 224, 263–265
darlingi	0.804	2	173
dirus	0.916	18	176, 207, 267–269
farauti	0.829	19	177, 266
flavirostris	0.961	9	176, 270
fluviatilis	0.735	27	167
freeborni	0.740	8	271
funestus	0.690	30	144, 257, 272–274
gambiae ss	0.860	36	42, 149, 185, 191, 192, 275, 276
labranchiae	0.850	17	195, 262
maculatus	0.800	10	157, 207, 277, 278
melas	0.860	6	(see An. gambiae)
messeae	0.881	14	261, 262
minimus	0.876	12	181, 207, 279
multicolor	0.865	15	219
muneztovari	0.766	11	49
pharoahensis	0.735	17	219
pseudopunctipennis	0.880	13	222
pulcherrimus	0.780	12	69, 227
punctulatus sl	0.855	7	177, 280
quadrimaculatus	0.966	27	222, 281, 282
sacharovi	0.858	47	261, 283
sergentii	0.950	18	215, 284
sinensis	0.857	21	243, 244
stephensi	0.810	37	166, 169, 170, 246, 263, 265
superpictus	0.945	18	283, 285
sundaicus	0.859	17	130, 157

sistent methodology than any biologic property. For the purpose of the present global analysis, therefore, we chose to substitute a fixed value for longevity.

The methodology generally used for defining the blood-feeding habit of a mosquito[286] is considerably less diverse and apparently more consistent than are methods used for estimating survival. Such estimates generally derive from precipitin resting, a method that has been used since the early 1920s and that has resulted in a considerable body of information on many of the dominant vectors. Because the precipitin test shows a relative lack of sensitivity,[286] such results tend to be less determinate than are those based on gel diffusion or gene amplification. However, this diversity in the methods used for discriminating between blood sources appears not to introduce bias.

Rationale for using a single representative vector. In characterizing regional force of transmission, we elected to base our calculations on the single most dominant anopheline species native to a particular place and during a given month. Not all possible vectors were included in the analyses because malaria prevalence rapidly becomes saturated as the entomologic inoculation rate increases.[287] The contribution of a single dominant vector captures virtually all of the "signal" that characterizes endemicity in a region, thereby rendering secondary vectors irrelevant. This reasoning is based on the

rationale that even subtle differences in human biting behavior and longevity lead to large differences in the force of transmission. These terms contribute powerfully in a nonlinear fashion. For similar reasons, additive weighting by relative abundance is avoided because a weak vector would unrealistically dilute the effect of the strong vector. A cumulative index that sums the contributions of all vectors would, similarly, be misleading.

Definition and contribution of a. Much of the regional variation in the stability of malaria transmission can be explained solely by reference to vector feeding behavior. Although this factor is not the most powerful component of vectorial capacity, it may vary most widely as an intrinsic property of diverse vector species. Feeding preference is strongly influenced by the availability of particular hosts, and certain innate and species-specific properties of the vector affect choice. These behaviors range from complete zoophily to complete anthropophily with a continuum of intervening gradations. Longevity, as a trait, varies more subtly than does blood-feeding habit.

The vectorial capacity term for anthropophilic biting behavior (a) is handled variously in the literature. The original approach[7] divided human biting preference by the length of the gonotrophic cycle in days to derive a term that specified the proportion of the vector mosquito population that actively sought hosts on a given day and likely to feed on human hosts. Various investigators depict a as the human biting rate. For the purpose of defining this index, however, we dissociate human feeding preference from biting interval because of the relative paucity of information on temperature-gonotrophic relationships for many mosquitoes. However, such temperature relationships are included in the index in the calculation for extrinsic incubation period length. Ideally, both temperature-dependent relationships would be included, thereby enhancing the differentiation between temperate and tropical regions because the current temperature effect would effectively be squared.

The effect of abundance and competence. Our index includes those factors that most powerfully and perennially influence the intensity of malaria transmission. Other vector characteristics, such as abundance and competence, affect transmission less powerfully. Mosquito abundance is also affected by extreme inter-annual and inter-spatial variation that would tend to obscure the innate epidemiologic capacities of different types of mosquitoes. For the dominant vectors specified in our index, competence is less variable, but similarly weak in its influence. Competence often separates into input and output components,[7] the probability that infected mosquitoes pass infection to a reservoir host (b) and the reverse relationship (c). Each of these terms, like abundance, has a linear effect on the force of transmission. Because we chose to ignore the contribution of less competent secondary vectors, the variation in competence between the vectors included in our index is greatly reduced. Our list of dominant vectors, therefore, represents an elite subset of the most competent anophelines capable of transmitting malaria.

The effect of other missing factors on the index. The resolution of our index might be sharpened by including other estimators. In highland and in arid sites, where malaria transmission is seasonal, the infectiousness of the human reservoir population may periodically become reduced. A reservoir competence factor that is adjusted for the duration of such

Stability index

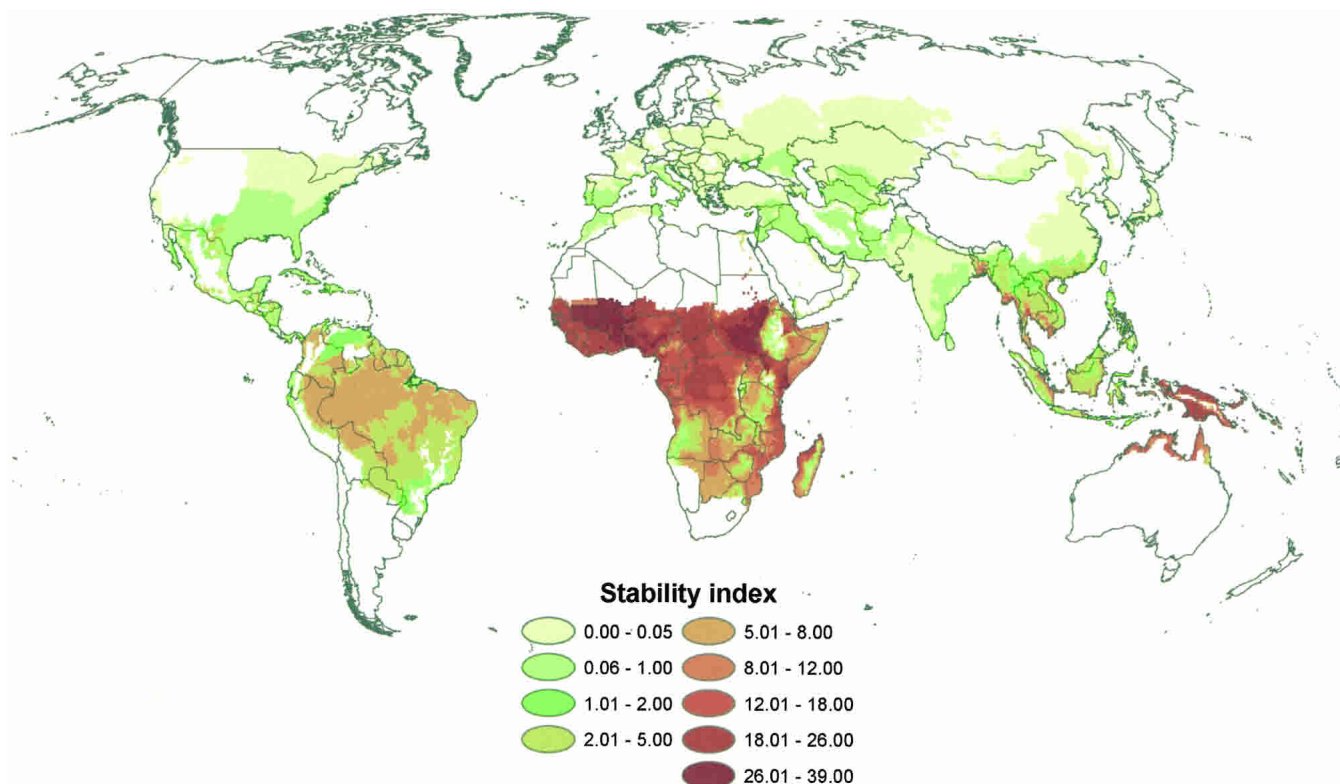|	
0.00 - 0.05	5.01 - 8.00
0.06 - 1.00	8.01 - 12.00
1.01 - 2.00	12.01 - 18.00
2.01 - 5.00	18.01 - 26.00
	26.01 - 39.00

FIGURE 2.   Distribution (Robinson projection) of the actual and potential stability of malaria transmission based on regionally dominant vector mosquitoes and a 0.5° gridded temperature and precipitation data set.

interruptions would tend to increase the contrast between the index values of temperate regions and those of highly seasonal tropical regions that include sites in which transmission is uninterrupted. Exophilic feeding behavior may also affect the force of transmission. Although difficult to quantify, endophilic vectors contribute more to malaria risk than do those that are exophilic. Incorporation of this property into our index might be useful.

Increasing the resolution of the grid cells to something less than the 0.5° dictated by our climate data would also improve the index. With more finely resolved geographic data, more spatial variability would be included, particularly for smaller countries and islands omitted due to the large size of each grid cell. The influence of focally important vectors such as urban *An. stephensi* and oasis-breeding *An. sergentii* would also be represented more accurately.

Anthropogenic conditions may modify our stability index by influencing the distribution, survival rate, and feeding habits of vectors. Insecticide use, improved house construction, land-use changes, and pollution (such as detergent contamination) would reduce the force of transmission. Anthropogenic changes that increase transmission would include accumulations of puddled ground water and enhanced resting sites. The latter condition can be a powerful determinant because it enhances longevity. Such artifactual conditions intermingle in a complex manner and would be difficult to incorporate into our index.

The contribution of the density of the human population to the stability of transmission might also be important because malaria transmission depends on the interaction of humans and mosquito vectors. Weighting by population density might reduce the index in countries where dense human populations inhabit non-malarious regions, such as the highlands of Kenya. In certain other regions, such as the Sahel, where people are compelled to reside where water is available, and thus where transmission is most stable, the index may become amplified. A parameter representing human density would contribute to the specificity of our stability index.

Effect of species complexes. Many of the more broadly distributed anophelines represent complexes of heterogeneous populations. Although our analysis would have benefited from the finest possible resolution of such complexity, certain of the parameters that we used were based on aggregated estimates. In the case of *An. fluviatilis*, for example, the hbi values clustered distinctly around two medians. The standard deviation in this case approaches or surpasses the corresponding mean, suggesting aggregation of heterogeneous populations. In the absence of evidence to the contrary or of a means of applying such evidence to our parameters, we treated such disparate estimates as though they represent values for a single homogeneous population.

Summing up. Our index of malaria stability depicts the regional resiliency of malaria perpetuation. It fills the gap between climatologically based and clinically based indices of transmission by including the most powerful components of vectorial capacity and their differing expression in the various anopheline vectors of malaria. Thus, it explicitly depicts the effects of ambient temperature on the force of transmission of malaria, as expressed through the length of the extrinsic incubation period, and the proportion of the vector population able to survive long enough to become infectious. Therefore, our map synthesizes the interaction of climate with malaria

pathogens and mosquito vectors more comprehensively than do maps based on climate or clinical incidence alone. Our index of malaria stability provides baselines for comparing regional infectious throughputs in malaria vectors. These indices can help in efforts to design antimalaria interventions and to explore the links between malaria intensity and economic development. One immediate use of the index is as a statistical control in studies of the effects of malaria on economic development. A traditional problem with analyses of the correlation between malaria endemicity and economic development is the tendency of causation to run in both directions: from malaria to poverty and from poverty to malaria. The new index will be useful in measuring the extent of causation running from malaria to poverty because the index can be used as an instrumental variable in regressions of economic growth and income levels on malaria endemicity. The first statistical results of this application underscore the importance of malaria as an important causal factor in chronic impoverishment of holoendemic regions.[288] Global variation in the stability of malaria transmission derives from interactions between climate and the specific biological characteristics of certain, dominant anopheline vectors.

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