

# A Climate-based Distribution Model of Malaria Transmission in Sub-Saharan Africa

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*Malaria remains the single largest threat to child survival in sub-Saharan Africa and warrants long-term investment for control. Previous malaria distribution maps have been vague and arbitrary. Marlies Craig, Bob Snow and David le Sueur here describe a simple numerical approach to defining distribution of malaria transmission, based upon biological constraints of climate on parasite and vector development. The model compared well with contemporary field data and historical 'expert opinion' maps, excepting small-scale ecological anomalies. The model provides a numerical basis for further refinement and prediction of the impact of climate change on transmission. Together with population, morbidity and mortality data, the model provides a fundamental tool for strategic control of malaria.*

There have been several attempts to define the global and national distributions of malaria<sup>1-3</sup>. Common to all previous attempts at mapping malaria risk is that they derive from a combination of expert opinion, limited data and the use of crude geographical and climate iso-lines. None has a clear and reproducible numerical definition: consequently, their comparative value is limited.

Recently, the tools for the spatial representation of events have improved with the availability of affordable geographical information systems (GIS) software and large global data sets including climate, population, satellite imagery and topography. Consequently, the mapping of environmentally determined diseases is receiving renewed interest<sup>4-13</sup>. It is into this milieu that the MARA/ARMA (Mapping Malaria Risk in Africa/Atlas du Risque de la Malaria en Afrique)<sup>14</sup> project was born. One of the first objectives of MARA/ARMA was to find the limits of distribution of stable malaria transmission.

Transmission and distribution of vector-borne diseases are greatly influenced by environmental and climatic factors. An indicator of malaria stability is the reproduction rate ( $R_0$ ) of the disease: when  $R_0$  is less than one, malaria is unstable, with a potential to die out; when  $R_0$  is greater than one, malaria is stable and likely to continue indefinitely. Vectorial capacity<sup>2,15</sup>, the main component in  $R_0$ , is strongly determined by climate. In this paper, the authors propose a 'fuzzy logic' model of the distribution of stable malaria transmission in sub-Saharan Africa. The model is based on the effect of mean rainfall and temperature on the biology of malaria transmission. Even though the relationships between transmission potential and disease outcome are ill defined<sup>16</sup>, Snow *et al.* (this issue) attempt to project burdens of malaria mortality for sub-Saharan Africa, using the model described here, in conjunction with selected mortality data.

## Fuzzy logic

Defining the precise edges of distribution of malaria is difficult owing to small-scale ecological variability and temporal changes in transmission risk. In reality there is a gradual, ill-defined transition from perennial to seasonal to epidemic to malaria-free regions, as well as from high to low transmission intensity. Malaria distribution is not definable in space, because the edge of distribution is indistinct, or in time, because both intensity and distribution wax and wane with the natural periodicity of events. It is not possible to predict, for each point in space, the probability of transmission occurring or not occurring, because many contributing factors such as mosquito density, human activities, human and vector genetics, etc. are not measurable or available at the continental scale. Of the available data surfaces, we consider climate to be the most important in limiting transmission and distribution of malaria on a large scale. Climate could be considered as either able or unable to sustain transmission. This would be a boolean situation, where climate is suitable (1) or unsuitable (0). Defining boolean thresholds above which the temperature-rainfall combination is considered suitable and where malaria is expected to occur, or below which malaria is expected not to occur, would be ignoring natural gradients and inherent uncertainty.

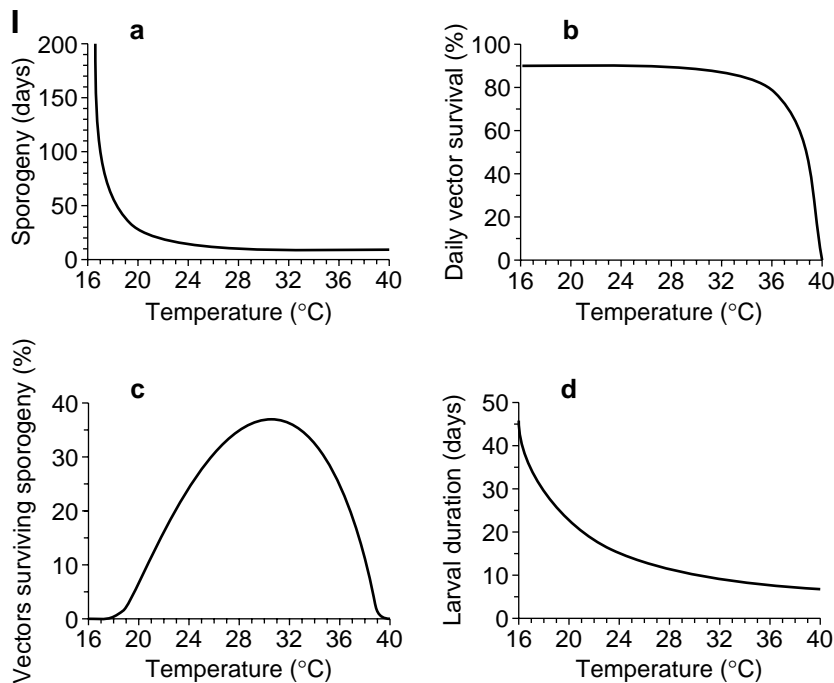
Fuzzy logic<sup>17</sup> is an extension of boolean logic that deals with the concept of partial truth or, put differently, the extent to which a statement is true (fractions between 0 and 1): climate is completely suitable, completely unsuitable, or in between, semi-suitable. While probability sets are fuzzy, i.e. non-boolean, fuzzy sets are not probabilities, because they do not necessarily add up to one, as do probabilities. Any 0-1 curve, considered appropriate for the subject, may be applied. The type of curve chosen depends mostly on what and how much is known about the suitability gradient.

## Continental climate

Continental monthly temperature and rainfall surfaces<sup>18</sup>, essentially interpolated weather station data, were used to provide the climate data. They represent long-term mean monthly profiles, i.e. monthly means in the average year. Conceptually, regions can be defined as: (1) perennial – where conditions are always suitable for transmission; (2) seasonal – where conditions become suitable for a short season every year; (3) epidemic – where long-term variation in climate renders conditions suitable for transmission on an irregular basis (with a potential of epidemic malaria); and (4) malaria-free – where conditions are always unsuitable. Because inter-annual variation is not reflected in long-term mean climate data, epidemic zones are not detectable. Using this data set to predict regions of annual transmission would lead to exclusion, at the fringe, of rare epidemic zones, but inclusion of frequent epidemic zones. More finite data (in space and time) is required to define the epidemic zones and this is being addressed presently.

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**Box 1. Relationships between Temperature and Sporogonic Duration ( $n$ ), Mosquito Survival ( $p$ ) and Larval Duration**



The effect of temperature on duration of the sporogonic cycle ( $n$ ) in days is defined as<sup>2,32</sup> (Fig. 1a, above):

$$n = \frac{DD}{T - T_{min}} \quad (1)$$

where  $DD$  is the total degree days for parasite development (111 for *Plasmodium falciparum*),  $T$  is the mean temperature in degrees centigrade and  $T_{min}$  is the temperature at which parasite development ceases (16°C for *P. falciparum*). High temperature speeds up mosquito development<sup>21</sup> and decreases the interval between bloodmeals, leading to more frequent host-vector contact<sup>28</sup>, but also reduces mosquito survival (D. le Sueur, PhD Thesis, University of Natal, 1991; R. Maharaj, PhD Thesis, University of Natal, 1995). Daily mosquito survival ( $p$ ) is defined by Martens<sup>11</sup> as:

$$p = e^{-1/(-4.4 + 1.31T - 0.03T^2)} \quad (2)$$

assuming constant humidity (Ib). Thus, the combined effect of  $n$  and  $p$  ( $p^n$ ) indicates the percentage of a vector cohort that survives the full period required for completion of sporogony at different temperatures (Ic). Another effect of temperature, namely on larval duration ( $ld$ ) in days, can be expressed as:

$$ld = 1 / (0.00554T - 0.06737) \quad (3)$$

and is shown in (Id). The formula is derived from data published by Jepson<sup>21</sup> and D. le Sueur (op. cit.)

and mosquito survival is sufficiently high (15%) for the transmission cycle to be completed. Thus, temperatures below 18°C were considered unsuitable, and above 22°C, suitable for stable transmission.

The upper limit of temperature suitability is determined by vector survival, as sporogony takes less than a week. Temperatures of above 32°C have been reported to cause high vector population turnover, weak individuals and high mortality (D. le Sueur, PhD Thesis, University of Natal, 1991; R. Maharaj, PhD Thesis, University of Natal, 1995). Thermal death for mosquitoes occurs around 40–42°C<sup>21,22</sup> and daily survival is zero at 40°C<sup>11</sup>.

In addition to average temperature, Leeson<sup>23</sup> found that in Zimbabwe, *Anopheles gambiae* s.l. disappeared when absolute minimum air temperature in winter fell below 5°C, and DeMeillon<sup>24</sup> found that in the old Transvaal province, South Africa (now Mpumalanga, Gauteng, North-West and Northern Province) vector distribution discontinued in areas that experienced frost. Stuckenberg<sup>25</sup> plotted effective temperature (an indicator that emphasizes the importance of summer temperature and length in terms of biological activity) against frost incidence in 84 weather stations. The highest effective temperature with at least one day of frost per annum was 16.4°C. In southern Africa the 16.4°C effective temperature iso-line compared well with the 5°C minimum temperature iso-line, the main differences occurring in parts of the Zimbabwean highlands and along a wide band across central Botswana. The 5°C minimum temperature iso-line was used here, bracketed on both sides by 1°C, to account for uncertainty, so that 6°C and above was suitable, 4°C and below, unsuitable.

## Temperature effects on transmission

The effects of temperature on the transmission cycle of the malaria parasite *Plasmodium falciparum* are manifold, but its specific effects on sporogonic duration ( $n$ ) and mosquito survival ( $p$ ) are the most important<sup>19,20</sup>. The mathematical relationships are shown in Box 1.

The lower limit of temperature suitability is determined by the number of mosquitoes surviving the incubation period ( $p^n$ ): while parasite development only ceases at 16°C, transmission below 18°C is unlikely because few adult mosquitoes survive the 56 days required for sporogony at that temperature, and because mosquito abundance is limited by long larval duration. At 22°C sporogony is completed in less than three weeks

## Rainfall effects on transmission

The relationship between mosquito abundance and rainfall is complex and best studied when temperature is not limiting. Studies have demonstrated the association between *An. gambiae* s.l. abundance and rainfall<sup>26,27</sup> (D. le Sueur, unpublished) but a direct, predictable relationship does not exist. *Anopheles gambiae* s.l. are seen to breed more prolifically in temporary and turbid water bodies, such as ones formed by rain<sup>28,29</sup>, while in permanent bodies predation becomes important<sup>30</sup>. By contrast, *A. funestus* prefer more permanent water bodies<sup>28</sup>. However, both temporary and permanent water bodies are dependent on rain. Rain is also related to humidity and saturation deficit: factors that affect

Box 2. Temperature and Rainfall Profiles of Selected Regions

Monthly climate data were extracted for selected sites (Fig. I) where the malaria epidemiology had been established:

**Stable malaria regions:** a, Siaya district, Kenya<sup>33</sup>; b, Ifakara area, Tanzania<sup>34</sup>; c, North KwaZulu-Natal, South Africa<sup>5</sup>; d, Niore du Sahel, Mali<sup>35</sup>.

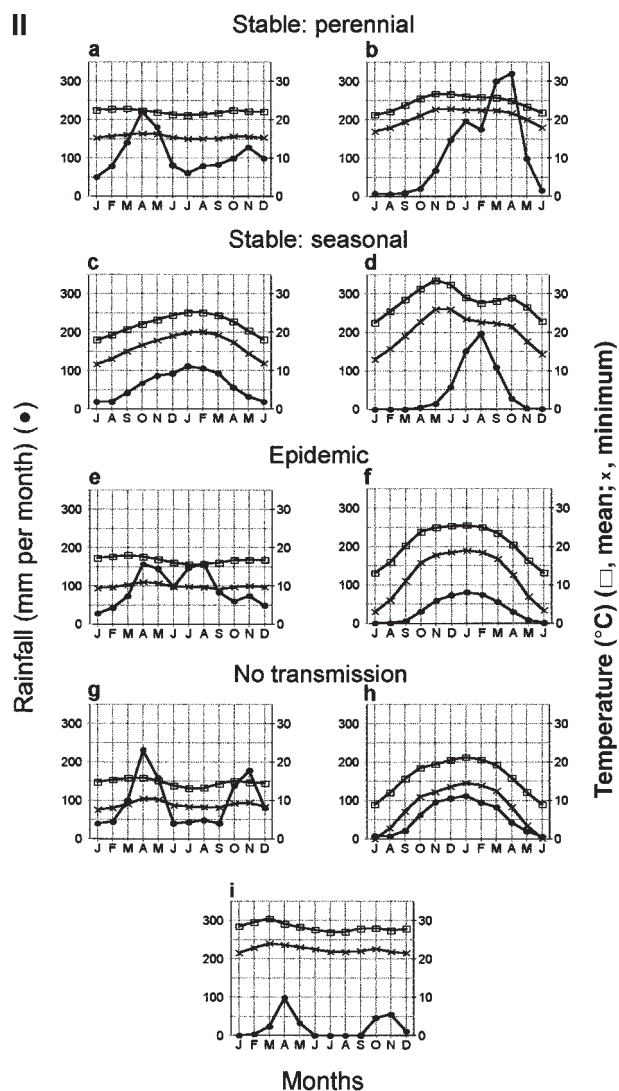
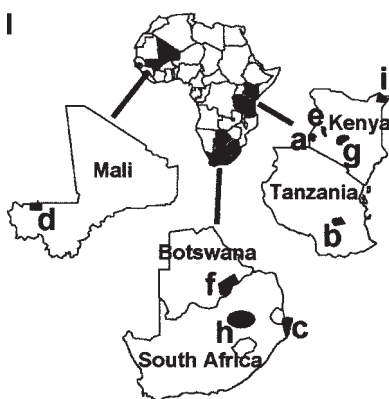
**Epidemic malaria regions:** e, Uasin Gishu district, Kenya<sup>36</sup>; f, Gaborone area, Botswana\*.

**Malaria-free regions:** g, Kenya western highlands<sup>†</sup>; h, Johannesburg area, South Africa<sup>‡</sup>; i, North-East Kenya<sup>†</sup>.

Graphs (Fig. II) of long-term mean temperature (open rectangles), minimum temperature (crosses) and rainfall (closed circles) profiles by month.

The effect of mean temperature is illustrated in Fig. IIa, IIe and IIg where rainfall is high all year: a constant temperature of 22°C in (IIa) is sufficient for perennial transmission, 18°C all year in (IIe) is too cold but epidemics occur in warmer years, while in (IIg), where mean temperature remains around 15°C, transmission never occurs. Similarly, mean temperatures in (IIc) and (IIh), which have the same seasonal rainfall pattern, suggest that seven months above 22°C allows seasonal transmission, while six months above 18°C does not.

In terms of rainfall, the difference between (IIc) and (IIf), which have similar mean temperature patterns, indicates that five months above 80 mm rain is sufficient, but five months above 60 mm is not. In (IIe) there is the added limiting effect of low minimum temperatures in winter, but rare epidemics do occur in particularly wet years<sup>37</sup>. It is further apparent from areas (IIe) and (IIi) that where temperatures are high, one month of rain above 80 mm is not sufficient for a transmission season, but that three months above 80 mm is.



\* Botswana Ministry of Health (1998) *Botswana Malaria Cases: District Data 1982-1994*

† UNICEF: Kenya Country Office, Government of Kenya (1994) *Vitamin A Deficiency in Kenya. A Report of the National Macronutrients Survey*

‡ Department of Health (1998) *South Africa; Malaria Case Records by District, 1983-1997*

mosquito survival<sup>26</sup>. There is good reason for using rainfall to indicate the probable presence of vectors, their survival and the potential for malaria transmission. Although it is known that flooding often causes destruction of breeding sites<sup>21</sup> and a temporary reduction of vectors, it never eliminates the vector, so that very high rainfall was still considered optimal for transmission. The amount of monthly rain required was examined by extracting the climate patterns in regions where the status of malaria was known.

### Diagnostic climate patterns

To examine the pattern of mean climate, as it relates to different epidemiological settings, monthly rainfall and temperature values were extracted from the climate data surfaces<sup>18</sup> for 20 different sites where malaria transmission has traditionally been regarded as perennial (annual, for more than six months), seasonal (annual, for less than six months), epidemic (transmission

not recorded every year) and malaria-free (malaria never recorded). The most diagnostic examples are displayed in Box 2.

The examples confirm that the approximate temperature cutoff point between epidemic and no-malaria zones is indeed around 18°C, and that 22°C allows stable transmission, while the difference between regions 'c' and 'e' (Box 2; Figs I and II, c and e) indicates a rainfall requirement for stable transmission of around 80 mm per month for at least five months.

The duration of the rainfall season is also important. In regions where temperature is high but rainfall is limiting, such as the fringes of the north African deserts, mosquito populations increase rapidly at the onset of rain, because of short developmental cycles. Consequently, three months of rain may be sufficient to constitute one transmission season. However, where temperature is limiting during the colder season, as is the case in large parts of southern Africa and highland



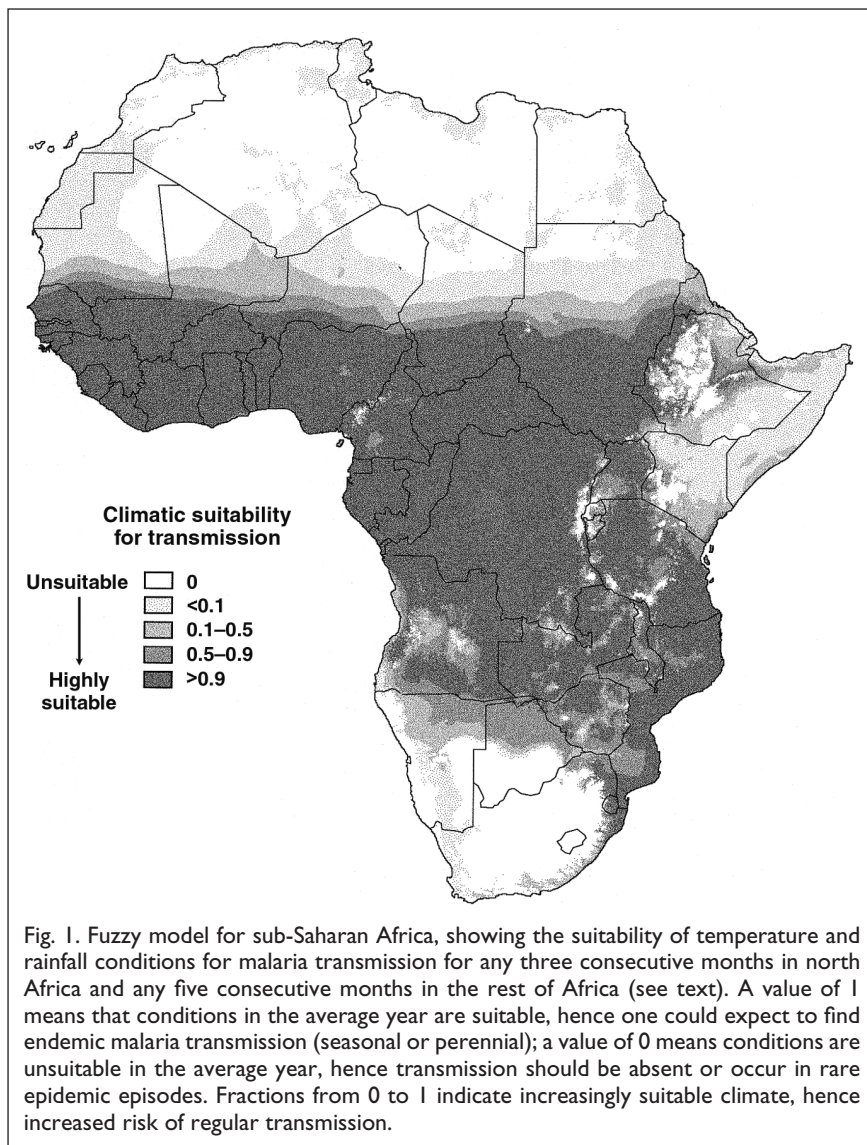


Fig. 1. Fuzzy model for sub-Saharan Africa, showing the suitability of temperature and rainfall conditions for malaria transmission for any three consecutive months in north Africa and any five consecutive months in the rest of Africa (see text). A value of 1 means that conditions in the average year are suitable, hence one could expect to find endemic malaria transmission (seasonal or perennial); a value of 0 means conditions are unsuitable in the average year, hence transmission should be absent or occur in rare epidemic episodes. Fractions from 0 to 1 indicate increasingly suitable climate, hence increased risk of regular transmission.

areas, mosquito populations increase slowly at the onset of rain, with gradually rising temperatures, owing to long developmental cycles. Parasite and vector development is slow, and favourable conditions need to last longer to provide a window of transmission. This is also illustrated by the extracted climate patterns: in Mali (Box 2; Figs I and II, d), where temperatures are always high, a three month window of high rainfall is sufficient for transmission, whereas in southern and eastern Africa (Box 2; Figs I and II, a–c), suitable conditions need to persist for at least five months.

## Constructing a fuzzy distribution model

The GIS raster software IDRISI and its FUZZY function were used to convert the climate data to climate suitability maps of fractions between 0 (conditions unsuitable,  $U$ ) and 1 (conditions suitable,  $S$ ). Initially, a simple sigmoidal fuzzy membership curve was used, defined in IDRISI as:

$$y = \cos^2 \left[ \frac{x - U}{S - U} \times \frac{\pi}{2} \right] \quad (4)$$

where  $y$  is the fuzzy suitability of climate value  $x$ . In the decreasing curve, fuzzy membership is equal to  $y$ , in the increasing curve it is  $(1 - y)$ . As outlined in the previous

Fig. 2 (right). Comparison of the model with southern African distribution data. The climatic model: 0, unsuitable; 1, suitable (a). Malaria maps show malaria risk in 1995 in Namibia (Richard Kamwi, Ministry of Health and Social Services, Namibia, pers. commun.), 1938 in South Africa<sup>5</sup> and annual malaria case numbers per district in Botswana (b). The Namibia risk map is an expert opinion map, based on case data. The Botswana map is based on microscope-confirmed case data collected at district level from 1982 to 1994. Malaria case incidence in South Africa (not shown here) between 1987 and 1993 has been above 1% just north and east of Swaziland, and 1% or less elsewhere, but because malaria control has considerably reduced malaria in South Africa<sup>5,38</sup> it is necessary to look at the historical map. Although the units in the maps of the three countries differ, agreement with the model is evident.

sections, for rainfall,  $U=0$ ,  $S=80$  mm per month; for average temperature  $U=18$ ,  $S=22^\circ\text{C}$  for the increasing curve and  $S=32$ ,  $U=40^\circ\text{C}$  for the decreasing curve. For winter minimum temperature (mean daily minimum of coldest month)  $U=4$ ,  $S=6^\circ\text{C}$ .

Because favourable temperature and rainfall conditions have to coincide temporally for transmission to occur, the 12-monthly fuzzy rain and temperature images were overlaid month-by-month. The minimum suitability rating was calculated at each point, according to whichever (rain or temperature) was more limiting.

Furthermore, suitable conditions have to occur for a certain 'time window', constituting a transmission season, long enough for vector populations to increase and for the transmission cycle to be completed. In north Africa ( $>8^\circ$  north) the highest value spanning any three, and in the rest of Africa any five, consecutive months was calculated. To adjust the model for the effect of frost<sup>23,24</sup>, the fuzzy minimum winter temperature was overlaid, again calculating the minimum fuzzy value. The resulting model (Fig. 1) shows the distribution of conditions more or less suitable for stable malaria transmission, lasting for at least five consecutive months (or three in north Africa) in the average year.

## Does the model agree with available data?

Comparing the model with historical maps and malaria case data in southern Africa (Fig. 2), and in Kenya and Tanzania (Fig. 3), the resemblance is striking. In southern Africa the edge of malaria distribution is well represented. The malaria-free east African highland regions (Fig. 3) are also clearly reflected in the model. In Kenya, the coastal and south-western endemic zones agree, as do the 'malaria near water' regions, too dry to register as suitable in the model. Minor discrepancies are discussed in the figure captions.



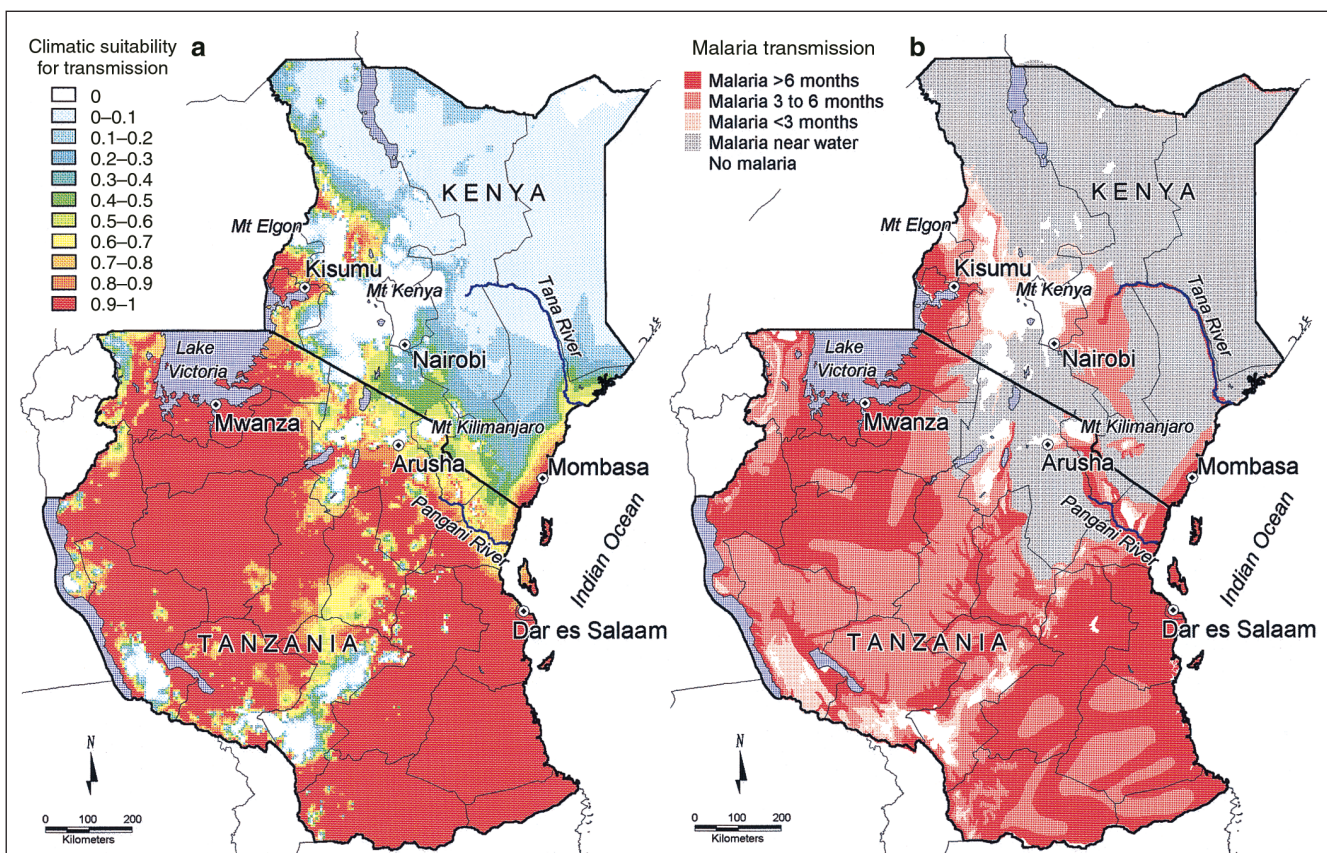
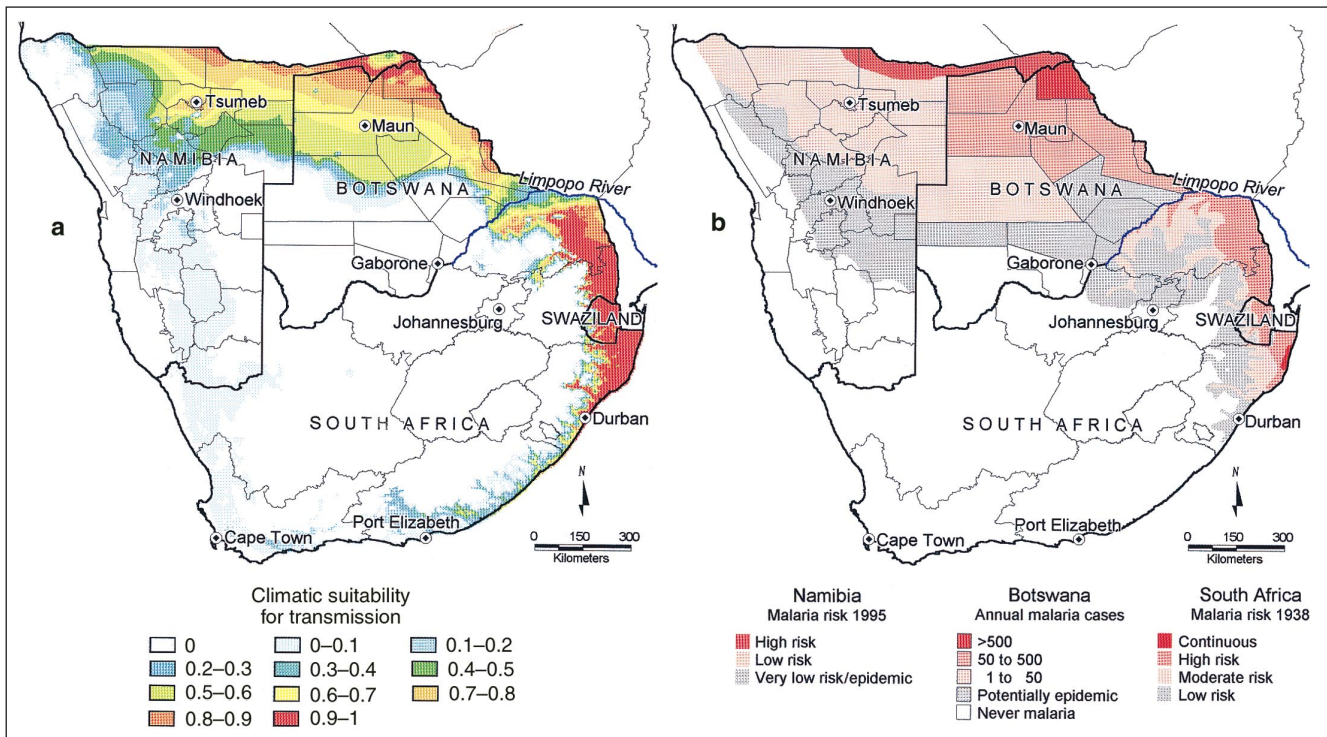


Fig. 3. Comparison of the model with Kenyan and Tanzanian malaria maps. The climatic model: 0, unsuitable; 1, suitable (a). Malaria maps of Kenya<sup>37</sup> and Tanzania<sup>39</sup> are shown in (b). Agreement between the model and the historical maps is good. The area southeast of Mount Kenya and Nairobi was historically recorded malarious for three to six months, whereas the model predicts low climatic suitability. On closer inspection, this area is found to be flat, low-lying country, which may receive additional run-off water from the adjoining highlands; a high normalized difference vegetation index (NDVI, which is a measure of the amount of photosynthesis taking place, and hence relates to the moisture availability, saturation deficit, soil properties and humidity) indicates an abundance of water. Nevertheless, empirical data from this region<sup>40</sup> suggest that malaria transmission is low and sporadic, and we have to question the accuracy of the historical map. The discrepancies in the Tana and Pangani (a and b above) river valleys, as well as the Limpopo river (Fig. 2), are a result of the model using only rainfall to predict the presence of vectors so that, although rainfall may be low, breeding sites are available and humidity is high along banks and floodplains of major rivers.

It is remarkable how such a simple model as this, driven by an understanding of the situation on the ground, approximates the edge of malaria distribution across the continent so well. Because we are looking at the distribution of stable malaria transmission, the edge of the suitable zone must be regarded as the lowest level of endemic malaria (hypo-endemic and/or strongly seasonal), where we expect to find substantial (not necessarily high) levels of transmission occurring every year. The situation within the suitable zone (fuzzy value 1) may vary from low to high transmission intensity, but this is not reflected in a distribution model. The situation outside the suitable zone (fuzzy values from 0.9 down to 0) reflects the gradient from stable to increasingly unstable transmission with lower and lower transmission intensity, until, at the outermost fringes, malaria becomes a sporadic, unpredictable event, subject to the chance influx of parasites in rare wet or warm years.

In Botswana, 13 years of incidence data\* show that districts in the same fuzzy zone behave similarly from year to year in terms of actual numbers of cases recorded. Reported cases clearly decline from the three endemic districts in the north, to extremely low numbers in the central district, where, in four out of 13 years, no cases were recorded at all. In a further five districts, malaria cases are reported in extremely rare years (David Rumisha, pers. commun.). The outlook of this model for public health applications is dealt with by R.W. Snow *et al.* (this issue).

Around the equator, rainfall patterns are slightly to strongly bimodal, some regions receiving rain in two short, distinct seasons. The model described above required five consecutive months with a rainfall above 80 mm. We ran the model again, with the same fuzzy definitions, but instead of looking for consecutive suitable months, calculated the maximum fuzzy values persisting for five months in total. The difference between the two models was 0 or negligible in most of Africa, except for parts of central, south-eastern and northern Kenya, and with very small differences in Ethiopia, Somalia, southern Cameroun and along the northern Angolan coast. In all other areas a bimodal rainfall pattern did not affect the outcome of the model, and even the affected areas in Kenya are mostly dry and unstable, indicating that two short, distinct rainy seasons are after all not sufficient for endemic malaria.

To refine the shape of the fuzzy curves, and the suitability cutoffs *S* and *U*, it may be necessary to distinguish between the north, where the limiting factor is rainfall only, and the rest of Africa, where the effect is a combination of rainfall and temperature. Equatorial regions, where the diurnal and annual temperature ranges are low, and where temperature is limited by altitude, might also need to be differentiated from the South, where temperature range is great and minimum temperature plays an important part, and where temperature is limited largely by latitude. It is worth noting here that no true gold standard is available. Historical maps and limited long-term malaria records have to suffice for comparative purposes.

## Modelling at different spatial levels

We have demonstrated that a simple climate-based model can be used to define the crude distribution of malaria transmission in Africa. This model functions at the continental level, a scale for which we believe the data sets and the methodological approach to be appropriate, but which will not take into account small-scale anomalies that might affect distribution, such as rivers and floodplains in areas of low rainfall, agricultural practice, deforestation, etc. It reflects a conservative estimate of distribution. The inclusion of other smaller-scale data sets (hydrology, human activity, etc.) may allow more detailed predictions, but requires a different approach.

Thus, we view the modelling of malaria in Africa as a four-tier approach: (1) the first level, at the continental scale, defines the broad distribution of disease based on climatic conditions in an average year; (2) the second level, at a sub-continental scale, refines the distribution at the periphery using annual data sets for higher temporal resolution, and takes into account differences between major malaria ecological zones; (3) the third level, at a regional or national scale, would involve relating parasite ratios to climate and other factors and defining the transmission intensity within a given zone of transmission ecology, such as perennial, seasonal or bi-seasonal transmission; and (4) the fourth level, at a scale of 30 km<sup>2</sup> and below, is a process that operates below the second administrative unit and seeks to define variation in transmission on a local scale. The lower one goes in scale, the more one is forced to consider whether the input required is justified by the scale at which one is working and the meaning that one is drawing from the product.

The model presented here, at the first level, introduces a new approach to the numerical definition of continental malaria distribution. The main benefit lies in the fact that it can be repeated, evaluated and refined over time, and can be manipulated mathematically in combination with other data sets such as population<sup>31</sup> to provide improved estimates of people at risk, which is essential for prioritizing health services (R.W. Snow *et al.*, this issue). Such a model provides a baseline against which climate change scenarios (eg. global warming) can be evaluated in the long term. We are moving from the hypothetical to the quantifiable.

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## The Evolution of Trophic Transmission

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*Parasite increased trophic transmission (PITT) is one of the more fascinating tales of parasite evolution. The implications of this go beyond cocktail party anecdotes and science fiction plots as the phenomenon is pervasive and likely to be ecologically and evolutionarily important. Although the subject has already received substantial review, Kevin Lafferty here focuses on evolutionary aspects that have not been fully explored, specifically: (1) How strong should PITT be? (2) How might sexual selection and limb autotomy facilitate PITT? (3) How might infrapopulation regulation in final hosts be important in determining avoidance of infected prey? And (4) what happens when more than one species of parasite is in the same intermediate host?*

Some of the most compelling Nature documentaries are those that show hunting and feeding behavior, such as a lioness downing a gazelle, or an osprey snatching a fish from the water's surface. Hidden from view and

never mentioned are the parasites that are experiencing transmission at that moment. Unfortunately, parasite transmission loses some of this drama when portrayed to undergraduates as arrows in a parasite life cycle. A perusal of life cycle diagrams in any parasitology text will reveal that many 'typical' (as in Ref. 1) parasites (many nematodes, most trematodes, most cestodes and all acanthocephalans) depend on a definitive host eating an intermediate host. Such trophic transmission is conspicuously absent in a few groups such as the monogeneans, gyrocoelid Cestodaria, rhabditoid, oxyuroid and filarial nematodes and schistosomatid trematodes<sup>2</sup>. Trophic transmission might have evolved under the strong selective pressure to survive the death of the host by predation, a feat most easily accomplished by parasitizing the host's predator. In addition to surviving, parasites able to succeed at this would typically enter a larger and longer-living host.

Many parasites that achieve transmission via the food chain alter the behavior or appearance of intermediate hosts to increase their risk of being preyed upon by final hosts (reviewed in Refs 3–6). Broad categorical

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