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The Ecology of *Anopheles* Mosquitoes under Climate Change: Case Studies from the Effects of Environmental Changes in East Africa Highlands

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Abstract

Climate change is expected to lead to latitudinal and altitudinal temperature increases. High elevation regions such as the highlands of Africa, and those that have temperate climate are most likely to be affected. The highlands of Africa generally exhibit low ambient temperatures. This restricts the distribution of *Anopheles* mosquitoes, the vectors of malaria, filariasis and O'nyong'nyong fever. The development and survival of larval and adult mosquitoes are temperature dependent, as are mosquito biting frequency and pathogen development rate. Given that various *Anopheles* species are adapted to different climatic conditions, changes in the climate could lead to changes in species composition in an area which may change the dynamics of mosquito-borne disease transmission. It is important to consider the effect of climate change on rainfall which is critical to the formation and persistence of mosquito breeding sites. In addition, environmental changes such as deforestation could increase local temperatures in the highlands; this could enhance the vectorial capacity of the *Anopheles*. This experimental data will be invaluable in facilitating the understanding of the impact of climate change on *Anopheles*.

1. Introduction

Anopheles mosquitoes are responsible for the transmission of a number of diseases in the world including malaria, lymphatic filariasis (*Wuchereria bancrofti* and *Brugia malayi*) and viruses such as one that causes O'nyong'nyong fever among others. In Africa, *Anopheles gambiae* is one of the best known vector species because of its prominent role in the transmission of the most dangerous malaria parasite species – *Plasmodium falciparum. Anopheles gambiae* sensu lato is a complex of at least seven morphologically indistinguishable sibling species. There are approximately 460 recognized *Anopheles* mosquito species worldwide and over 100 of them are capable of transmitting human or animal diseases.

Anopheles mosquitoes, being poikilotherms, have life history characteristics that are dependent on ambient temperatures. These life history characteristics include their biting rates, the duration of their gonotrophic cycles, their fecundity, the survival and development

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of the immature mosquitoes and the adult. Thus, any factor that can alter any of these characteristics has the capacity to affect the disease transmission potential of the mosquitoes. Environmental changes, climate variability, and climate change are such factors that could affect the biology and ecology of *Anopheles* vectors and their disease transmission potential.

Climate change is expected to lead to latitudinal and altitudinal temperature increases. Future global warming projections indicate that the best estimate of surface air warming for a “high scenario”, is 4.0 °C with a likely range of 2.4- 6.4 °C by 2100 [1]. Such a temperature increase will alter the biology and ecology of many mosquito vectors and subsequently, the dynamics of the diseases they transmit. Because arthropods critically depend on ambient temperature for survival and development [2], their distribution range is often limited by temperature. For example, in the highelevation areas or highlands of Africa, ambient temperature is low, restricting the development and survival of *Anopheles* mosquitoes. However, climate warming or any factor that alters the microclimatic conditions of *Anopheles* mosquitoes (e.g., deforestation) in the highlands may facilitate the persistence of the mosquito population there [3]. Furthermore, changes in precipitation and humidity are also expected to occur under climate change scenarios; the synergistic effects between temperature and precipitation are expected to have major effects on the ecology of *Anopheles* mosquitoes and mosquito-borne diseases [4]. Increased precipitation may affect larval habitat availability and stability, and habitat productivity [5]. The association between precipitation, vector abundance, and malaria prevalence has been well supported [6].

Mosquito populations in the highlands may be more sensitive to climate change than those in the lowland areas of Africa. Climate warming can mediate mosquito physiology and metabolic rate because metabolic rate increases exponentially rather than linearly with temperature in ectotherms [7]. Therefore, *Anopheles* mosquitoes in highland areas are expected to experience a larger shift in metabolic rate due to the effects of climate warming. Climatic conditions affect *Anopheles* mosquitoes in a number of ways. The development rate of immature mosquitoes is highly dependent on temperature. Low-temperature conditions result in severe delays in larval development and can also result in high mortality. Below 16°C, larval development of *Anopheles gambiae*, the main malaria vector in most parts of Africa, will stop; the larvae will die in water temperature below 14°C [8]. When water temperature rises, the larvae take a shorter time to mature [9] and consequently, there is a greater capacity to produce more offspring. In the adult stage, an increase in ambient temperature will accelerate the digestion of blood meals taken by mosquitoes, leading to increased human biting frequency, faster parasite sporogonic development [10], translating to an increased disease transmission efficiency [11]. Increased biting frequency and faster blood meal digestion also mean increased fecundity and better reproductive fitness [12]. However, temperature above 34°C generally has a negative impact on the survival of vectors and parasites [13].

Anthropogenic environmental changes such as deforestation, urbanization, and agricultural practice may have significant effects on mosquito habitat availability, microclimatic conditions of the aquatic habitats and human residences where adult mosquitoes rest. This review will focus on the impact of anthropogenic environmental changes on the ecology of *Anopheles* vectors and malaria disease transmission in African highlands. It gives the perspective of changes in climate as a result of anthropogenic environmental changes could be likened to climate change and is expected to increase our understanding of how climate change could impact on the ecology of *Anopheles* mosquitoes.

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2. Impact of land use and land cover changes on *Anopheles* mosquito biology and ecology

In many parts of the world, especially in Africa and South America, anthropogenic environmental changes, such as deforestation, have been linked to altered malaria transmission dynamics. Deforestation for the purposes of logging and self-subsistence agriculture is a serious problem in the tropical regions of Africa [14]. For example, Malava forest, a tropical rainforest in Kakamega district, Kenya, shrank from 150 km^2 in 1965 to 86 km^2 in 1997 [15]. In the East African highlands, 2.9 million hectares of forest were cleared between 1981 and 1990, representing an 8% reduction in forest cover in one decade [16]. Land use and land cover changes may modify the temperature and relative humidity of malaria vector habitats in the highlands. It was demonstrated that in the southwestern highlands of Uganda, maximum and minimum temperatures were significantly higher in communities bordering cultivated swamps than in those near natural swamps [16]. These changes in regional climate and in the microclimatic conditions of mosquito habitats cause abundant changes in the existing mosquito species, and may make some areas permissive to the proliferation of new species. Land use and land cover changes have been linked to changes in vector ecology and malaria transmission. For instance, deforestation in Cameroon caused the introduction of *An. gambiae* into a habitat that was previously dominated by *An. moucheti* [17]. In northern Brazil, *An. marajoara,* a species previously of minor importance, became the principal malaria vector following changes in land use [18].

A series of studies were conducted in western Kenyan highlands to determine the influence of land use and land cover changes on the microclimatic condition of human residences, and subsequently on the ecology of *An. gambiae* mosquitoes, the primary malaria vector in the region [5]. The examined parameters included the duration of gonotrophic cycle, biting frequency, fecundity and survivorship, and sporogonic development of *Plasmodium falciparum* malaria parasite. The study area was originally forested, but has experienced severe deforestation for agricultural development in the past three decades. Deforestation increased the indoor mean temperature by 1.8°C. Mean maximum and minimum temperatures were increased by 2.3 and 1.5°C, respectively. Mean maximum outdoor temperature was significantly higher by 1.4°C in the deforested site than in the forested site (31.3 vs 29.9 °C). Mean outdoor temperatures were significantly higher by 1°C in the deforested site than in the forested site (19.9 vs 18.9°C). The mean indoor relative humidity in the deforested area was about 22.6% lower (79.88% vs. 57.29%) than in the forested area during the dry seasons [11]; [12]; [3]; [10].

The changes in the microclimatic conditions in the human residences induced by deforestation, significantly shortened the duration of the mosquitoes' gonotrophic cycle by 1.7 days (4.6 vs 2.9 days) [11]. The duration of the gonotrophic cycle is the period between the taking of a blood meal by a mosquito, including the digestion of the blood meal, until oviposition or egg laying [19]. The decreased duration of the gonotrophic cycles implies an increase in human biting frequency from an average of once every 5 days to once every 3 days. An increase in the biting frequency means that the *An. gambiae* will feed more frequently on humans and enhance malaria transmission potential exponentially. The microclimatic changes also shortened the sporogonic development time from an average of 14 days down to 12.6 days [10]. Both oocyst and sporozoite development times were reduced by 1 and 1.4 days respectively. Reduced parasite development time in mosquitoes indicates that the parasite took a shorter time to become infectious and therefore, is transmitted much more efficiently.

However, the changes in the microclimate due to deforestation did not favor the survival of the adult *An. gambiae*. The effect of deforestation decreased median survival of *An.*

gambiae by 5-7 days. The *An. gambiae* mosquito prefers areas with high humidity; since deforestation caused a decrease in indoor humidity, it decreased the median survival of *An. gambiae*. However, despite the decreased survivorship of the mosquitoes due to the effects of deforestation, mosquitoes exhibited an enhanced reproductive fitness by 40% over the course of mosquito life span [12], partly due to faster blood-meal digestion and more frequent blood-feeding. The implication of these findings is that *An. gambiae* could increase its population within a short time when breeding sites are available. This could potentially lead to an increase in malaria transmission when infected humans are available.

The findings in the western Kenyan highlands are consistent with the findings by other investigators in other African highland sites. In the highlands of Uganda, Lindblade and others [20] compared mosquito density, biting rates, sporozoite rates, and entomological inoculation rates between eight villages located along natural papyrus swamps and eight villages located along swamps that have been drained and cultivated. They found that on average all malaria indices were higher near cultivated swamps. Maximum and minimum temperatures were significantly higher in communities bordering cultivated swamps. The average minimum temperature of a village was significantly associated with the number of *Anopheles gambiae* per house. Thus, replacement of natural swamp vegetation with agricultural crops led to increased temperatures and elevated malaria transmission risk in cultivated areas.

Land use and land cover changes also affected the microclimatic condition of mosquito larval habitats. Munga and others [21] compared the microclimatic conditions and *An. gambiae* larval development and survivorship in semi-natural larval habitats under three land cover types (farmland, forest, and natural swamp). They found significantly higher water temperatures in farmland habitats as compared to the other land cover types. The mosquito pupation rate was significantly greater in farmland habitats than in swamp and forest habitats while larval-to-pupal development times were significantly shorter. Land cover type may affect larval survivorship and habitat productivity through its effects on water temperature and nutrients in the aquatic habitats.

It is important to note that the effects of land use and land cover on malaria vectors discussed above may be specific to African highlands where low ambient temperature is the major limiting factor for vector development and reproduction and sporogonic development of malaria parasites. Meta-analysis on the impact of environmental changes on the development and reproduction of malaria vectors that include large number of study sites and various anopheline species may reveal general principle on the effects of environmental changes on malaria vectors and the underlying biological mechanisms [22]

3. Proliferation of mosquito species to new areas

Global climate warming may render suitable the high-altitude areas previously unsuitable for proliferation of the mosquito vector population. Each mosquito species has its own minimum niche requirement, and one important limiting factor for the spatial distribution range is climate. For instance, *Anopheles arabiensis,* the sibling species to *An. gambiae*, is either absent or shows a very low abundance in high-altitude areas. Chen and others [23] reported *An. arabiensis* mosquitoes breeding in the central Kenyan highlands of elevation of 1,720 – 1,921 m above sea level for the first time, suggesting the local climate or ecological conditions have become conducive to the proliferation of malaria vector species. The consequence of new vector species persistence on malaria transmission may be significant and warrants careful and long-term vector and malaria monitoring.

Land use and land cover may modify the microclimatic conditions of the mosquito vectors which may further facilitate the population establishment and persistence in areas previously unsuitable for the mosquito vectors. For example, Manga and others [17] observed that deforestation for airport construction in Cameroon caused the introduction of *An. gambiae* into a habitat that was previously dominated by *An. moucheti*. In northern Brazil, *An. darlingi* is generally the dominant vector. However, land use and land cover changes made *An. marajoara,* a species previously of minor importance, the principal malaria vector [18]. This vector species is highly susceptible to malaria infection and exhibits anthropophilic biting behaviour. Changes in vectorial system pose novel and special challenges to malaria control due to the presence of various species with different resting and feeding behaviours and various extents in susceptibility to insecticides.

Afrane and others [3] used the life-table analysis to investigate whether climate conditions in the western Kenyan highlands were permissive to the development and survival of *An. arabiensis* and whether deforestation promoted *An. arabiensis* larval and adult survivorship. They found that the mean water temperature of aquatic habitats in the deforested area was 4.8–6.1°C higher than that in the forested area, *An. arabiensis* larval-to-adult survivorship was increased by 65-82 % they also noted that the larval-to-adult development time was shortened by 8–9 days as a result of deforestation. Deforestation is not solely responsible for such effects on microclimatic conditions and mosquito larval survival due to reduced canopy coverage. For example, Munga and others [21] found that larval development time was significantly shortened in breeding sites in farmlands compared to breeding habitats in natural swamps in the western Kenyan highlands.

Deforestation also enhanced the survivorship and reproductive fitness of adult *An. arabiensis* mosquitoes in the highlands [3]. The average indoor temperature in the houses in the deforested area was 1.8°C higher than in the forested area, and the relative humidity was 22–25% lower. The median survival time of adult mosquitoes in the deforested area was 49–55% higher than those in the forested area and the net reproductive rate of female mosquitoes in the deforested area was 1.7- to 2.6-fold higher than that in the forested area. As a result, *An. arabiensis* placed in the deforested area had better survival and laid more eggs to produce more offsprings. The implications of these findings are that, if the current trends of deforestation continue in the highlands, *An. arabiensis* could invade, inhabit, and proliferate in the highlands. The establishment and persistence of *An. arabiensis* in the highlands could worsen the malaria situation because of the resilience demonstrated by this vector species to control measures such as insecticide-impregnated bed-nets or indoor residual spray methods.

4. Climate warming and malaria resurgence in the East African highlands

The conventional wisdom is that climate plays a large role in malaria especially in transition regions such as highlands and desert fringes where temperature and rainfall limit the abundance of mosquitoes. However, there have been strong debates over the last decade on whether climate warming has occurred in the East African highlands and whether climate is a driving force for a series of malaria epidemics observed in the 1990s in this region [24]. Hay *et al*. [24] concluded that mean temperature and rainfall have not changed significantly in the past century at four locations in the East African highlands, where malaria incidence has been increasing. Pascual *et al*. [25] reanalyzed the temperature trend data in the same East African sites and found evidence for a significant warming trend at all sites - a rise of approximately 0.5 degrees celsius in the last half of the 20th century. Omumbo *et al*. [26] used over thirty years of quality-controlled daily observations of maximum, minimum and mean temperature in the analysis of trends at Kericho meteorological station, situated in Kenya's western highlands. They found that an upward trend of approximately 0.2°C/decade could be observed in all three temperature variables. Mean temperature variations in the Kericho area were associated with large-scale climate variations including tropical sea surface temperatures (SST). Local rainfall was found to have inverse effects on minimum and maximum temperature. They also used three versions of a spatially interpolated temperature data set, which showed markedly different trends when compared with each other and with their data. This study intimates that the increases in temperatures observed in the East African region, could be attributed to the effects of climate change and environmental changes.

The effect of climate change on the epidemiology of malaria is less conspicuous. Given that malaria transmission depends on vector abundance, mosquito biting rate, vector survivorship, and parasite sporogonic rate, changes to the ambient temperature may affect many or all of these factors. Loevinsohn [27] assessed the contribution of the climate to a malaria epidemic in the late 1980s in Rwanda. In late 1987, malaria incidence in the area increased by 337% over the three previous years. He found that the increase was greatest in groups with little acquired immunity – children under two years and people in high-altitude areas. An autoregressive correlation analysis found that temperature, especially mean minimum, best predicted incidence at higher altitudes where malaria had increased most. Alonso *et al*. [28] developed a dynamic model that incorporated the population dynamics of the mosquito vector with the temperature time series and found that a small increase in ambient temperature has a major but nonlinear effect on malaria transmission. In parallel, climate variability, defined as short-term fluctuations around the mean climate state, is associated with clinical malaria incidence in the East African highlands despite a high spatial variation in the sensitivity of malaria incidence to climate fluctuations in the highlands [29]. Interestingly, temperature and rainfall exhibited nonlinear and synergistic effects on malaria incidence. Wanjala *et al* [30] found that topographic and drainage features could explain the different malaria transmission rates in different western Kenyan highland areas with similar climate and elevation.

An often used but unreliable indicator of malaria incidence is clinical malaria cases taken from hospital records. The unreliability of this indicator stems from variations in health seeking behavior, health policy, human immunity, drug resistance and other related factors. In order to measure the impact of climate warming on malaria transmission potential, one can use vectorial capacity (C). Vectorial capacity is defined as the daily rate at which future inoculations arise from a currently infective case [31]; this can be seen as a true measure of malaria transmission potential. Vectorial capacity is expressed as:

$$C=\frac{ma^2pn}{-Log(P)}$$

where *m* is the relative density of vectors in relation to humans, *a* is the average number of humans bitten by one mosquito in one day, *p* is the proportion of vectors surviving per day, and *n* is the duration of sporogony in days. Afrane *et al*. [10] found that deforestation nearly doubled the vectorial capacity in western Kenyan highlands (Table 1).

As observed, deforestation greatly facilitates malaria transmission in western Kenyan highlands; one would expect reforestation or other methods of increasing canopy coverage for aquatic habitats to reduce malaria transmission. Indeed, Wamae *et al*. [32] showed that in western Kenyan highlands, shading habitats by growing Napier grass around mosquito breeding habitats reduced the temperature of aquatic habitats by as much as 5°C, which significantly reduced habitat productivity by more than 85%. Forests have been shown to stabilize local temperatures and reforestation can help in mitigating the effects of climate change on malaria.

Predicting the potential regions where malaria distribution will be extended to or whether malaria will return to areas where it had previously been endemic but has been eliminated incurs a large uncertainty. Such predictions are largely based on models that did not take into consideration of the ecology and complex behavior of both humans and vectors [33], heath-seeking behavior changes, health policy changes, improvement or degradation of health infrastructure and other factors that impact malaria epidemiology. Furthermore, there are large intrinsic spatial heterogeneities in the response of malaria transmission dynamics to climate changes [34]. For example, in sites of relatively low altitude (<1600m above sea level) in western Kenya highland, malaria trends and temporal variability began to decrease in the late 1980s. However, at higher altitudes (>1600 m elevation), regime shifts reflected an increase in malaria transmission intensity in the 1980s and 1990s as well as an increase in variability [34]. Because of large spatial heterogeneities and paucity of good-quality long-term malaria epidemiological data in African highlands, spatially and temporally fine-grained data in malaria case dynamics and vector dynamics as well as contextual information on other malaria intervention parameters will be extremely valuable for predicting the impacts of climate change on malaria transmission.

5. Conclusions

Climate change has multifaceted effects on malaria transmission in the African highlands where temperature and rainfall limit the abundance of mosquitoes. Climate warming may make the areas previously too cool for vector population establishment now suitable, causing an expansion of vector species to higher-altitude areas. Warm climate may facilitate larval development, enhance vector survivorship and reproductive fitness, and increase the blood feeding frequency and parasite sporogonic development rate in the previously cooler highlands. These effects have been explained using scenarios from anthropogenic environmental changes in east Africa and other parts of the world. Environmental changes, either natural or anthropogenic, alter the ecological balance and context within which vectors and their parasites breed, develop, and transmit diseases [35], and may facilitate or reduce malaria transmission. Deforestation in the western Kenyan highlands exhibited strong positive effects on the development and survival of *An. gambiae* and *An. arabiensis* mosquito larvae, enhanced the survivorship of adult mosquitoes, increased human feeding frequency and shortened the development time of the parasites through effects on the microclimatic condition of the mosquitoes. It is important to note that climate change is also involved with abnormal rainfall patterns. Synergistic effects between temperature and rainfall on vector ecology and malaria transmission may be produced. Climate warming is expected to have continental or regional effects on malaria transmission while the influence of environmental changes on malaria transmission is local and may be site-specific. As climate warming and environmental changes may have a longterm effect on malaria transmission, it is imperative to conduct systematic, long-term surveillance in various sentinel sites in Africa and other continents on climate, vector dynamics and community structure, and malaria transmission dynamics. This experimental data will be invaluable in helping to understand the impact of climate change on malaria and also helping to develop an effective approach in controlling malaria.

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References

1. IPCC. Climate Change 2007: Impacts, Adaptation, and Vulnerability Cambridge Univ Press. 2007

2. Lindsay SW, Birley MH. Climate change and malaria transmission. Ann Trop Med Parasitol. 1996; 90:573–588. [PubMed: 9039269]
3. Afrane YA, Zhou G, Lawson BW, Githeko AK, Y G. Life-table analysis of Anopheles arabiensis in western Kenya highlands: effects of land covers on larval and adult survivorship. A m J Trop Med Hyg. 2007; 7:660–666.
4. Githeko AK, Lindsay SW, Confalonieri UE, Patz JA. Climate change and vector-borne diseases: a regional analysis. Bull World Health Organ. 2000; 78:1136–1147. [PubMed: 11019462]
5. Githeko AK, Ndegwa W. Predicting malaria epidemics in the Kenya highlands using climate data: a tool for decision makers. Global Change and Human Health. 2001; 2:54–63.
6. Dery DB, Brown C, Asante KP, Adams M, Dosoo D, et al. Patterns and seasonality of malaria transmission in the forest-savannah transitional zones of Ghana. Malar J. 2010; 9:314. [PubMed: 21054895]
7. Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL. Effects of size and temperature on metabolic rate. Science. 2001; 293:2248–2251. [PubMed: 11567137]
8. Koenraadt CJM, P KP, S P, Githeko AK, Takken W. Low level vector survival explains unstable malaria in the western Kenya highlands. Tropical Medicine and International Health. 2006 in press.
9. Munga S, Minakawa N, Zhou G, Githeko AK, Yan G. Survivorship of immature stages of Anopheles gambiae s.l. (Diptera: Culicidae) in natural habitats in western Kenya highlands. J Med Entomol. 2007; 44:758–764. [PubMed: 17915505]
10. Afrane YA, Little TJ, Lawson BW, Githeko AK, Yan G. Deforestation Increases the Vectorial Capacity of Anopheles gambiae Giles to Transmit Malaria in the Western Kenya Highlands. Emerg Infect Dis. 2008 In Press.
11. Afrane YA, Lawson BW, Githeko AK, Yan G. Effects of Microclimatic Changes Due to Land use and Land Cover on the Duration of Gonotrophic Cycles of Anopheles gambiae Giles (Diptera: Culicidae) in Western Kenya Highlands. Journal of Medical Entomology. 2005; 42:974–980. [PubMed: 16465737]
12. Afrane YA, Zhou G, Lawson BW, Githeko AK, Yan G. Effects of Microclimatic Changes Due to Deforestation on the Survivorship and Reproductive Fitness of Anopheles gambiae in Western Kenya Highlands. Am J, Trop Med Hyg. 2006; 74:772–778. [PubMed: 16687679]
13. Rueda LM, Patel KJ, Axtell RC, RE S. Temperature-dependent development and survival rates of Culex quinquefasciatus and Aedes aegypti (Diptera: Culicidae). J Med Entomol. 1990; 27:892–898. [PubMed: 2231624]
14. Ernst KC, Lindblade KA, Koech D, Sumba PO, Kuwuor DO, et al. Environmental, socio-demographic and behavioural determinants of malaria risk in the western Kenyan highlands: a case-control study. Trop Med Int Health. 2009; 14(10):1258–1265. [PubMed: 19772547]
15. FAO. Forest resources assessment, 1990: Tropical countries. FAO forestry paper No112; Rome, Italy: 1993.
16. Lindblade KA, Walker ED, Onapa AW, Katungu J, Wilson M, et al. Land use change alters malaria transmission parameters by modifying temperature in a highland area of Uganda. Trop Med Int Health. 2000; 5:263–274. [PubMed: 10810021]
17. Manga L, Toto JC, Carnevale P. Malaria vectors and transmission in an area deforested for a new international airport in southern Cameroon. Societes Belges Medicine Tropicale. 1995; 75:43–49.
18. Conn JE, Wilkerson RC, Segura MN, de Souza RT, Schlichting CD, et al. Emergence of a new neotropical malaria vector facilitated by human migration and changes in land use. Am J Trop Med Hyg. 2002; 66:18–22. [PubMed: 12135261]
19. Santos RL, Forattini OP, Burattini MN. Laboratory and field observations on duration of gonotrophic cycle of Anopheles albitarsis s.l. (Diptera: Culicidae) in southeastern Brazil. J Med Entomol. 2002:926–930. [PubMed: 12495194]
20. Lindblade KA, O'Neill DB, Mathanga DP, Katungu J, Wilson ML. Treatment for clinical malaria is sought promptly during an epidemic in a highland region of Uganda. Trop Med Int Health. 2000; 5:865–875. [PubMed: 11169276]
21. Munga S, Minakawa N, Zhou G, Githeko AK, Y G. Survivorship of immature stages of Anopheles gambiae s.l. (Diptera: Culicidae) in natural habitats in western Kenya highlands. J Med Entomol. 2007:758–764. [PubMed: 17915505]

22. Sinka ME, Bangs MJ, Manguin S, Coetzee M, Mbogo CM, et al. The dominant Anopheles vectors of human malaria in Africa, Europe and the Middle East: occurrence data, distribution maps and bionomic précis. Parasit Vectors. 2010; 3:117. [PubMed: 21129198]
23. Chen H, Githeko AK, Zhou G, Githure JI, Yan G. New records of Anopheles arabiensis breeding on the Mount Kenya highlands. indicate indigenous malaria transmission. Malar J. 2006; 7:17. [PubMed: 16522206]
24. Hay SI, Cox J, Rogers DJ, Randolph SE, Stern DI, et al. Climate change and the resurgence of malaria in the East African highlands. Nature. 2002; 415:905–909. [PubMed: 11859368]
25. Pascual M, Ahumada JA, Chaves LF, Rodo X, Bouma M. Malaria resurgence in the East African highlands: temperature trends revisited. Proc Natl Acad Sci U S A. 2006; 11:5635–5636.
26. Omumbo JA, Lyon B, Waweru SM, Connor SJ, Thomson MC. Raised temperatures over the Kericho tea estates: revisiting the climate in the East African highlands malaria debate. Malar J. 2011; 10:12. [PubMed: 21241505]
27. Loevinsohn ME. Climatic warming and increased malaria incidence in Rwanda. Lancet. 1994; 343:714–718. [PubMed: 7907685]
28. Alonso D, Bouma MJ, Pascual M. Epidemic malaria and warmer temperatures in recent decades in an East African highland. Proc Biol Sci. 2011; 278:1661–1669. [PubMed: 21068045]
29. Zhou G, Minakawa N, Githeko AK, Yan G. Association between climate variability and malaria epidemics in the East African highlands. Proc Natl Acad Sci U S A. 2004; 101:2375–2380. [PubMed: 14983017]
30. Wanjala CL, Waitumbi J, Zhou G, AK G. Identification of malaria transmission and epidemic hotspots in the western Kenya highlands: its application to malaria epidemic prediction. Parasit Vectors. 2011; 4:81. [PubMed: 21595898]
31. MacDonald, G. The Epidemiology and Control of Malaria. Oxford University Press; Oxford: 1957.
32. Wamae PM, Githeko AK, Menya DM, Takken W. Shading by napier grass reduces malaria vector larvae in natural habitats in Western kenya highlands. Ecohealth. 2010; 7:485–497. [PubMed: 20602147]
33. R P. Global warming and malaria: knowing the horse before hitching the cart. Malar J. 2008; 7(Suppl 1):S3. Review. [PubMed: 19091037]
34. Chaves LF, Hashizume M, Satake A, Minakawa N. Regime shifts and heterogeneous trends in malaria time series from Western Kenya Highlands. Parasitology. 2011 Oct 14.:1–12.
35. Patz JA, Graczyk TK, Geller N, Vittor AY. Effects of environmental change on emerging parasitic diseases. Int J Parasitol. 2000; 30:1395–1405. [PubMed: 11113264]

Table 1

Estimated vectorial capacity of *Anopheles gambiae* in forested and deforested areas in western Kenya highland. Adapted from Afrane *et al.* (2008).

Land use type	*m*	*a*	*n*	*P*	Vectorial capacity
Forested	3.05	0.198	13.9	0.927	0.54
Deforested	4.64	0.233	12.8	0.917	0.96

Note. m is the relative density of vectors in relation to humans; P is the proportion of vectors surviving per day; a is the average number of men bitten by one mosquito in one day; n is the duration of sporogony in days.