Key Points:
- Dams are known to exacerbate malaria transmission, but its precise mechanisms are poorly understood, hindering effective control measures
- Wind and distance to shoreline were identified as key environmental factors that are important for malaria transmission around reservoirs
- In water-abundant highland regions, warmer temperature can significantly increase malaria risk, without increasing vector populations

Environmental Determinants of Malaria Transmission Around the Koka Reservoir in Ethiopia

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Abstract New dam construction is known to exacerbate malaria transmission in Africa as the vectors of malaria—*Anopheles* mosquitoes—use bodies of water as breeding sites. Precise environmental mechanisms of how reservoirs exacerbate malaria transmission are yet to be identified. Understanding of these mechanisms should lead to a better assessment of the impacts of dam construction and to new prevention strategies. Combining extensive multiyear field surveys around the Koka Reservoir in Ethiopia and rigorous model development and simulation studies, environmental mechanisms of malaria transmission around the reservoir were examined. Most comprehensive and detailed malaria transmission model, Hydrology, Entomology, and Malaria Transmission Simulator, was applied to a village adjacent to the reservoir. Significant contributions to the dynamics of malaria transmission are shaped by wind profile, marginal pools, temperature, and shoreline locations. Wind speed and wind direction influence *Anopheles* populations and malaria transmission during the major and secondary mosquito seasons. During the secondary mosquito season, a noticeable influence was also attributed to marginal pools. Temperature was found to play an important role, not so much in *Anopheles* population dynamics, but in malaria transmission dynamics. Change in shoreline locations drives malaria transmission dynamics, with closer shoreline locations to the village making malaria transmission more likely. Identified environmental mechanisms help in predicting malaria transmission seasons and in developing village relocation strategies upon dam construction to minimize the risk of malaria.

1. Introduction

Increasing dam construction is adding threat to malaria control efforts worldwide. Some 160 to 320 new large dams are estimated to be constructed annually around the world, a high percentage of which are now in African countries (International-Rivers, 2010; World Commission on Dams, 2000), where more than 90% of the world's malaria burden occurs. Reservoirs behind dams provide breeding sites for *Anopheles* mosquitoes—vector of malaria—and makes malaria transmission more likely (Castellanos et al., 2016; Jobin, 1999; Keiser et al., 2005; Kibret et al., 2009, 2015; Pommier de Santi et al., 2016; Sow et al., 2002; U.S. Public Health Service Tennessee Valley Authority, 1949; Yewhalaw et al., 2009). A systematic literature review by Keiser et al. (2005) reported that the creation of dams increases the number of malaria cases and altered the seasonality of malaria from seasonal to year-round transmission worldwide. Kibret et al. (2015) estimated that at least 15 million people live in proximity (<5 km) to reservoirs of large dams in sub-Saharan Africa; and that out of the 2.7 million annual malaria cases in those areas, 1.1 million cases are attributable to the existence of the reservoirs. The number of people at risk and of cases associated with large dams will increase due to increasing construction of dams, population growth, and climate change (Kibret et al., 2015, 2016).

Despite the apparent risk of malaria around dams and reservoirs, little assessment has been done, and few countermeasures implemented in practice to address the associated health concerns. This inaction may arise since the adverse health impacts are overlooked due to large economic return of dams or perhaps practical measures to reduce the risk of malaria are missing (Endo et al., 2015; U.S. Public Health Service Tennessee Valley Authority, 1949). Increasing need for dams and reservoirs calls for better understanding of the mechanisms of malaria transmission and better assessment tools to address the enhancement of malaria around reservoirs.

One of the environmental determinants that influences malaria transmission intensity around reservoirs is the distance to reservoirs. Closer proximity of a village to a reservoir is associated with higher number

of annual malaria cases because mosquitoes' lifetime flight distance limits malaria transmission far away from their breeding sites (Bomblies, 2014; Cano et al., 2006; Endo & Eltahir, 2016; Gu et al., 2006; Minakawa et al., 2002; Trape et al., 1992; van der Hoek et al., 2003; Zhou et al., 2007). For example, around the Koka Reservoir (N8°25′; E39°05′) in Ethiopia, the annual malaria case rates among people living within 1 km of the reservoir was 2.9 times greater than those living between 1 and 2 km from it, and 19.9 times greater than those living 5 to 9 km from it (Kibret et al., 2009).

While annual case rates are associated with the villages' proximity to reservoirs, intraannual seasonality of malaria case rates also suggests that there exist other environmental factors that are important in malaria transmission dynamics. Around the Koka Reservoir, a strong seasonality in *Anopheles* population and malaria transmission is observed (Endo, 2017; Kibret et al., 2009). Detailed analysis of the impacts of environmental factors on malaria transmission dynamics will provide better understanding of environmental mechanisms of malaria transmission around reservoirs, and hence aid more effective interventions.

This paper aims to investigate environmental mechanisms of malaria transmission around reservoirs. Combining extensive multiyear field surveys around the Koka Reservoir, rigorous model development, and simulation studies, the contributions of various environmental factors to malaria transmission around the reservoir are examined.

2. Materials and Methods

2.1. Study Site

This study was conducted at Ejersa, which is located northwest of the Koka Reservoir (N8°25′; E39°05′) in Ethiopia (Figure 1). This area is located at the Ethiopian Rift Valley and has been targeted for extensive field campaigns on environmental conditions and malaria transmission (Endo, 2017; Kibret et al., 2009). Ejersa has three seasons: the main rainy season from mid-June to mid-September, the secondary rainy season from March to May, and the dry season for the rest of the year. The annual rainfall is around 600–880 mm, with significant interannual variability. The temperature is slightly lower in the rainy season than in the dry season, with an annual temperature of around 21°C.

Anopheles populations peak twice in a year: a larger peak in September–December (hereafter, the *major mosquito season*) and a smaller peak in May–July (hereafter, the *minor mosquito season*). The major vectors present at Ejersa are *An. arabiensis, An. pharoensis, An. funestus*, and *An. coustani* (Endo, 2017; Kibret et al., 2009).

The annual incidence rate in this village was 55 (cases/1,000 persons/yr) between 2009 and 2014 (our data collection). Of the cases, approximately two thirds are caused by *Plasmodium falcipalum* (*Pf*) and one third by *Plasmodium vivax* (*Pv*). Malaria in this area is classified as hypoendemic, and the incidence rate is declining owing to control measures in place.

Ethiopia is keen on constructing dams and reservoirs. Its diverse topography and sufficient rainfall gift the country with a large hydropower potential. The Koka Dam was the first dam in Ethiopia, commissioned in 1960 primarily for hydropower generation. The reservoir is now used for multiple purposes, and it supplies about 6% of the national grid power as of 2014. Ethiopia is planning to accelerate dam construction, targeting to increase its hydropower generation from the current level of 1,500 MW to 17,000 MW by 2020 and to 35,000 MW by 2037 (Export.gov, 2017). Many more dams and reservoirs are expected to be constructed in the near future in Ethiopia with a looming potential for malaria increase.

2.2. Data Collection

Extensive field surveys were conducted from July 2012 to April 2015. Meteorological data (temperature, humidity, rainfall, wind speed, wind direction, and solar radiation), soil moisture data, and groundwater table data were obtained every 30 min from our own in situ stations (Figures 2 and 3). The daily water levels of the Koka Reservoir were provided by the Ethiopian Electric Power Corporation (Figure 3f). Adult mosquito populations were monitored using six CDC miniature light traps weekly around the main rainy season (June–December) and biweekly for the rest of the year (January–May). The abundance of aquatic-stage mosquitoes were also monitored at the same frequency at identified larval habitats (dipping pools in Figure 2) and reservoir shorelines. The mosquitoes collected were classified at the genus level (i.e., *Anopheles* or *Culex*) using the naked eye by trained local assistants; *Anopheles* mosquitoes were further classified by gender. More details of data collection methods can be found in Text S1 in the supporting information.
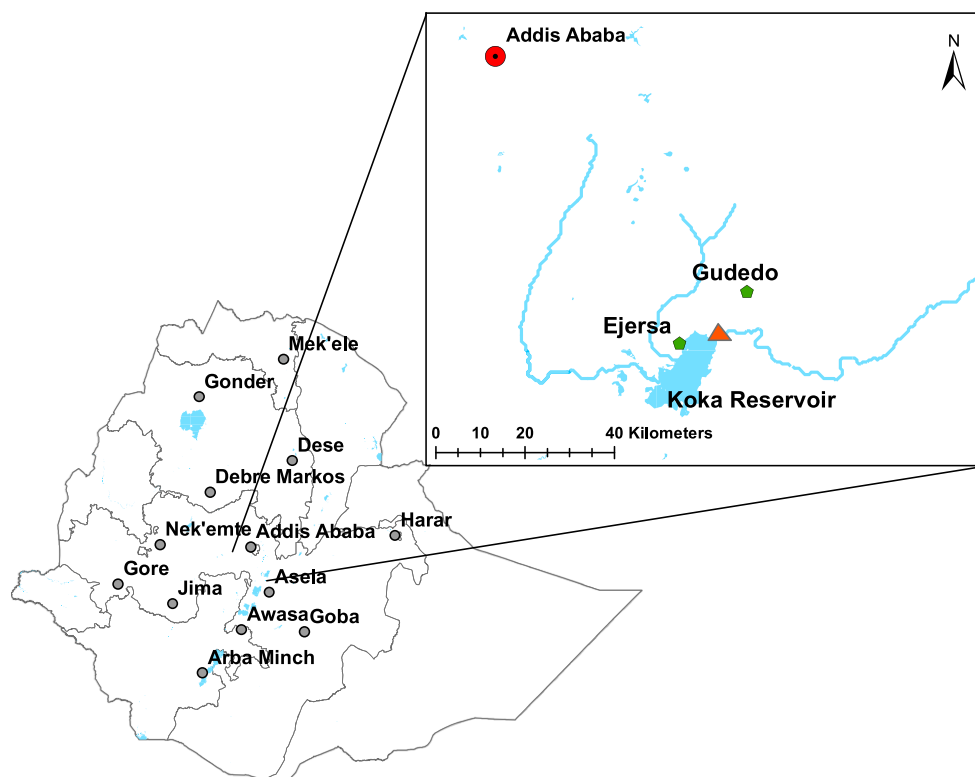
Figure 1. Location of the field site. The Koka Reservoir is located at the center of Ethiopia, approximately 80 km southeast of Addis Ababa. The water bodies crossing the country from northeast to southwest indicates the location of the Ethiopian Rift Valley. The Koka Dam is marked with an orange triangle at the northeast of the reservoir and is connected to the Awash River. Ejersa is adjacent to the reservoir and located northwest of the reservoir.

Climatic conditions during the main rainy season (from mid-June to mid-September) are described as low temperature, high humidity, and high wind speed. During this period, the reservoir water levels increase rapidly at the rate of about 10 cm/d. On the other hand, the secondary rainy season (from March to May) is characterized as having high temperature, relatively low humidity, low wind speed, and low reservoir water levels. During the dry season (from October to February), temperature, humidity, and wind speed stay relatively low. Wind direction changes before and after the main rainy season. Wind blows from the southwest during the main rainy season and from the east for most of the rest of the year. Wind direction changes gradually from east to southwest during the secondary rainy season.

2.3. Malaria Transmission Model

In order to examine malaria transmission mechanisms around a reservoir, the Hydrology, Entomology, and Malaria Transmission Simulator (HYDREMATS) was extended to simulate environment influenced by a reservoir system (Bomblies et al., 2008; Endo, 2017). HYDREMATS is a village-scale malaria transmission model, and it is one of the most detailed and comprehensive mechanistic malaria models to date(Reiner et al., 2013). Coupling modules that describe mechanistically hydrology, entomology, and malaria transmission, HYDREMATS can simulate explicitly in space and time: (1) presence of vector breeding pools, (2) life cycle of *Anopheles* mosquitoes, (3) behaviors of adult mosquitoes, (4) development of parasites, and (5) development of human immunity (Figure 4).

Presence of vector breeding pools. The presence of vector breeding pools is simulated by resolving hydrological processes (e.g., rainfall, evaporation, infiltration, and surface runoff) mechanistically. HYDREMATS simulates four types of breeding pools: rain-fed pools, groundwater(GW)-fed pools, marginal pools, and reservoir shoreline. Rain-fed pools are simulated combining a distributed flow routing to simulate surface runoff and the land surface scheme (LSX) (Foley et al., 1996; Pollard & Thompson, 1995) to simulate evapotranspiration (Bomblies et al., 2008). GW-fed pools form when the groundwater table becomes higher than the topography. Near large reservoirs, groundwater tables are influenced by the water levels of the reservoir, and the groundwater flow
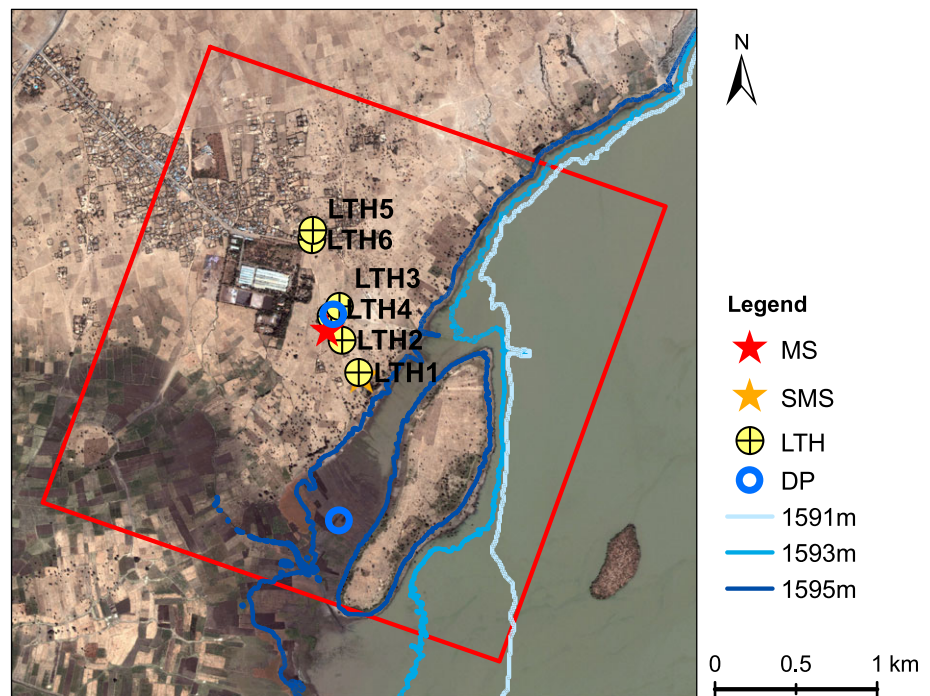
Figure 2. Field setting in Ejersa. Our field site, Ejersa, was equipped with the Meteorological Station (MS) (red star), the Soil Moisture Station (SMS) (orange star), and the mosquito light traps (yellow circle with cross). To measure the groundwater tables in Ejersa, pressure transducers were installed in small wells created adjacent to the MS and the SMS. Light traps were placed indoors and outdoors. Light trap houses (LTHs) with indoor operations and outdoor operations were labeled with odd and even numbers, respectively. The locations of dipping pools (DPs) are indicated by blue circles, where larvae samples were taken. The locations of shorelines were estimated for the reservoir water levels of 1,591 m (light blue), 1,593 m (sky blue), and 1,595 m (dark blue), based on the topography data. The change in shoreline is relatively small (a few hundred meters) at the north of the simulation domain (red rectangle), but is significant (as large as a kilometer) at the south of the domain. A large shift in the shorelines occurs at water levels between 1,583 m and 1,595 m. The red rectangles show the 3 km-by-3 km simulation domains.

direction can be approximated as one dimensional (Text S2) (Endo, 2017). Marginal pools are subgrid-scale water bodies that form adjacent to the shoreline. The formation of the marginal pools can be explained by the combination of muddy rough surface, shallow GW table, and high capillary fringe, and thus simulated accordingly (Text S2 and Figure S1). Reservoir shoreline can be simulated based on the topography and the reservoir water levels. Shoreline is the only part of a reservoir that is used for *Anopheles* breeding sites because the shallow water near shoreline offers larvae-rich nutrient, vegetation for protection, weak wave action, and low predation risk(Jobin, 2011).

Life cycle of Anopheles mosquitoes. Mosquitoes goes through the aquatic stage to the adult stage. The development and survival of aquatic-stage mosquitoes are simulated following Depinay et al. (2004). Adult survival rate is simulated as a function of temperature (Martens, 1997) and also of humidity (Endo, 2017; Yamana & Eltahir, 2013) (Text S2 and Figure S2).

Behaviors of adult mosquitoes. In the agent-based entomology model, behaviors of mosquitoes are simulated for each individual mosquito. Behaviors of mosquitoes simulated include host-seeking flight, blood meals, breeding-pool-seeking flight, and oviposition. Modeling of *Anopheles'* flight behavior is fully described in Endo and Eltahir (2018). All the activities of *Anopheles* mosquitoes are simulated in a spatially explicit manner.

Development of parasites. Malaria transmission requires *Anopheles* mosquitoes to undergo both mosquito stages (also known as (aka) extrinsic incubation period or EIP) and human liver stages (aka intrinsic incubation period or IIP). During mosquito stages, gamatocytes ingested from infectious person need to develop to sporozoites to be injected to a person. The EIP is a function of temperature and is parasite dependent (Detinova, 1962; Lindsay & Birley, 1996). Human-to-mosquito transmission efficiency and mosquito-to-human
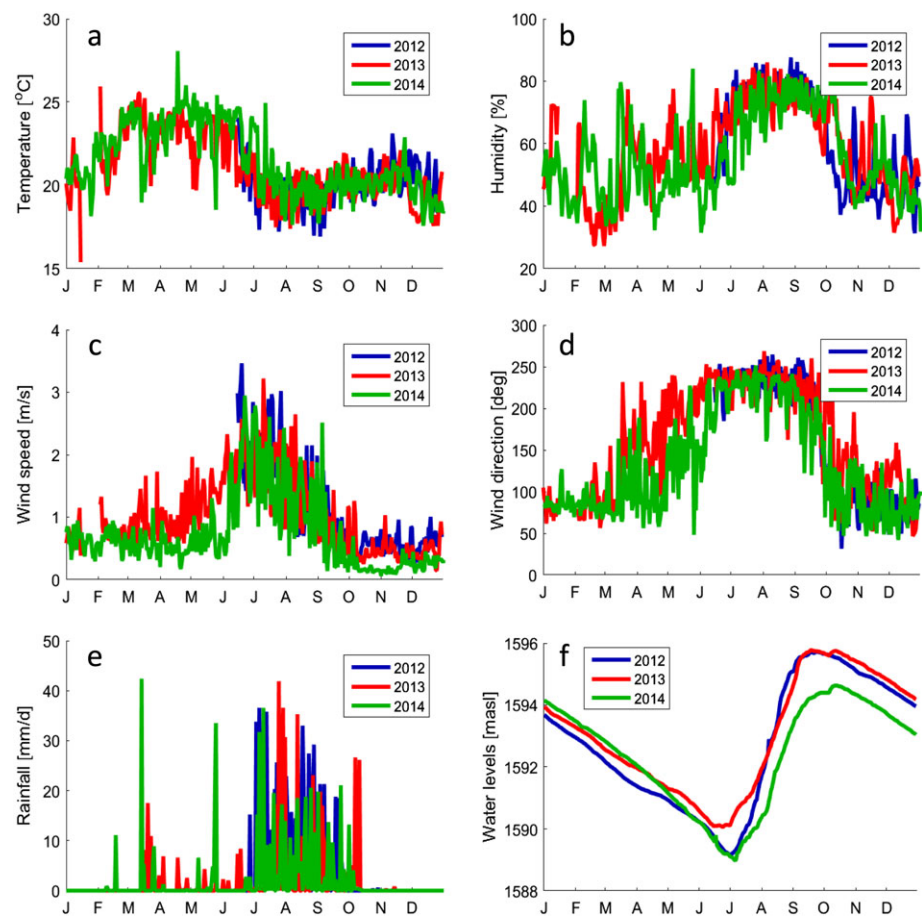
Figure 3. Observed environmental conditions at Ejersa. Observed (a) daily temperature [°C], (b) relative humidity [%], (c) wind speed [m/s], (d) wind direction [deg, clockwise from the north], (e) rainfall [mm/d], and (f) reservoir water levels [meter above sea level (masl)] are shown for 2012 (blue), 2013 (red), and 2014 (green).

transmission efficiency are also parasite dependent (Bharti et al., 2007; Jun et al., 2012). Parameters used in this study are found in Text S2.

Development of human immunity. Simulation of human immunity borrows from Yamana et al. (2013). People acquire immunity with infectious bites and gradually lose it with time. The transmission efficiency and malaria recovery rate are simulated taking account the levels of human immunity.

2.4. Model Application to Ejersa

The spatially and temporally explicit mechanistic model of HYDREMATS is most suitable for analyzing the environmental determinants of malaria transmission. HYDREMATS was applied to Ejersa (3 km-by-3 km simulation domain shown as red square in Figure 2) through the period of January 2012–April 2015 (hereafter *Ejersa model*), and shown to reproduce the dynamics of local environment, *Anopheles* populations, and malaria transmission (Text S3 and Figures S3–S6) (Endo, 2017). For details of the simulation results, see Text S3. The *Anopheles* populations and malaria transmission peaks twice in a year: around June and October. Environmental factors driving these dynamics are examined in the following method.

2.5. Contribution of Environmental Factors

In order to quantify contribution of environmental factors to malaria transmission dynamics around the Koka Reservoir, simulation studies were conducted, decomposing the impacts of environmental factors. These factors include temperature (*temp*), relative humidity (*rh*), wind speed (*wspd*), wind direction (*wdir*), rain-fed pools (*RFPs*), marginal pools (*MGPs*), and shoreline (*sln*). GW-fed pools were not observed nor simulated for Ejersa.

The simulation settings are summarized in Table 1. The fixed *temp*, fixed *rh*, fixed *wspd*, and random *wdir* models, removed variability of temperature, relative humidity, wind speed, and wind direction, respectively,
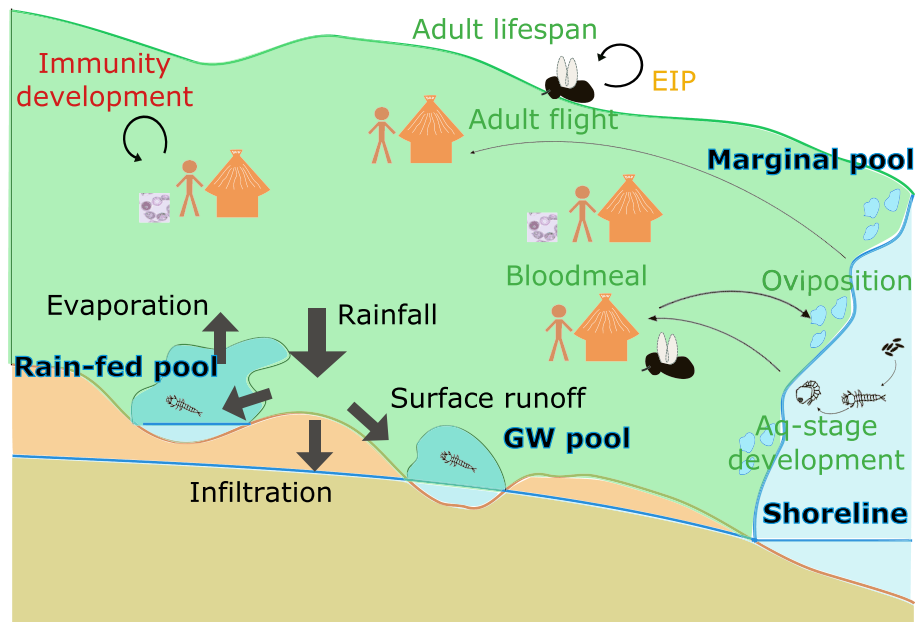
Figure 4. Schematic of Hydrology, Entomology, and Malaria Transmission Simulator (HYDREMATS). HYDREMATS is a comprehensive malaria transmission simulator, coupling hydrology, entomology, and malaria transmission modules. This village-scale model simulates surface pools explicitly both in space and time through the use of detailed topography data and representation of hydrological processes (e.g., rainfall, evaporation, infiltration, surface runoff, and groundwater flow). It simulates four types of pools: rain-fed pools, groundwater (GW)-fed pools, marginal pools, and reservoir. The entomology module is an agent-based model, which simulates the life cycle (e.g., aquatic-stage development and adult lifespan) and behaviors (e.g., blood meals, flight, and oviposition) of individual mosquito. Development of parasites (extrinsic incubation period) and human immunity are also simulated. The locations of houses, where mosquitoes take blood meals, are also simulated in a spatially explicit manner.

Table 1
Experimental Setup in Investigating the Contributions of Environmental Factors

	Climate factors				Breeding sites		
	temp	*rh*	*wspd*	*wdir*	*RFPs*	*MGPs*	*sln*
	∘: obs.	∘: obs.	∘: obs.	∘: obs.	∘: pres.	∘: pres.	∘: obs.
Model name	×: fixed	×: fixed	×: fixed	×: rand.	×: abs.	×: abs.	×: fixed
Ejersa model	∘	∘	∘	∘	∘	∘	∘
Fixed *temp*	×	∘	∘	∘	∘	∘	∘
Fixed *rh*	∘	×	∘	∘	∘	∘	∘
Fixed *wspd*	∘	∘	×	∘	∘	∘	∘
Random *wdir*	∘	∘	∘	×	∘	∘	∘
No *RFPs*	∘	∘	∘	∘	×	∘	∘
No *MGPs*	∘	∘	∘	∘	∘	×	∘
Sln only	×	×	×	×	×	×	∘
Fixed *sln*	∘	∘	∘	∘	×	×	×

Note. Based on the Ejersa model, the impacts of environmental factors were analyzed decomposing each factor. For temperature (*temp*), relative humidity (*rh*), wind speed (*wspd*), and shoreline (*sln*), either observed (∘) or fixed (×) values were applied. For wind direction (*wdir*), observed values (∘) or random values (×) were used. Regarding the rain-fed pools (*RFPs*) and the marginal pools (*MGPs*), simulations were conducted in the presence (∘) or absence (×) of respective water bodies.
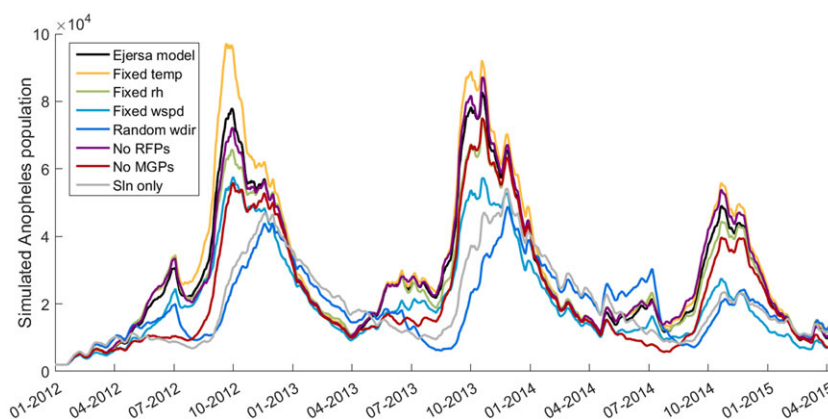
Figure 5. Simulated time series of the *Anopheles* population in investigation of the effects of environmental factors. Based on the Ejersa model, the contributions of climatological factors and the presence of breeding sites to the *Anopheles* population dynamics are evaluated. The results from the Ejersa model, fixed *temp* model, fixed *rh* model, fixed *wspd* model, random *wdir* model, no *RFPs* model, no *MGPs* model, and *sln*-only model are shown in black, orange, green, light blue, blue, purple, maroon, and gray, respectively.

from the Ejersa model, by using either fixed or random values instead of observed values (i.e., values with seasonal variability). The fixed *temp* model replaced the simulation forcing of observed temperature with the average temperature of the simulation period (1,200 days), 21.47°C, throughout the simulation time steps (i.e., no seasonality in temperature exists in the simulation). In the fixed *rh* model, a fixed value of relative humidity — 55.03%, the average observed relative humidity of the period — was used for model forcing instead of observational values. In the fixed *wspd* model, a fixed value of 0.88 m/s, which is the observed mean wind speed of the simulation period, was applied. The random *wdir* model applied a random wind direction every hour throughout the simulation period. The impact of each factor can be understood by the deviation between the Ejersa model and the respective simulation. The no *RFPs* model and the no *MGPs* model removed *RFPs* and *MGPs* from simulations, respectively. The *sln*-only model investigated the impact of the change in shoreline independent of all other environmental factors by removing the variability of climate factors and the presence of other breeding pools. Finally, the fixed *sln* model analyzed the impact of climatological factors, independent of the conditions of water bodies, by removing *RFPs* and *GWPs* and by fixing the location of shoreline.

3. Results

3.1. Contribution of Environmental Factors

The simulated time series of the *Anopheles* population is presented in Figure 5: the Ejersa model in black, the fixed *temp* model in orange, the fixed *rh* model in green, the fixed *wspd* model in light blue, the random *wdir* model in blue, the no *RFPs* model in purple, the no *MGPs* model in maroon, and the *sln*-only model in gray. Large deviations from the Ejersa model are apparent in the fixed *wspd* model, the random *wdir* model, and the no *MGPs* model, suggesting significant contribution of the wind and marginal pools to the dynamics of *Anopheles* populations.

The gap between the Ejersa model (black) and the *sln* only model (gray) should be explained by the variability of the environmental factors (i.e., *temp, rh, wspd*, and *wdir*) and the seasonal presence of the *RFPs* and *MGPs*. The contribution of each environmental factor to the gap is illustrated in Figure S7.

A large contribution from wind was found throughout a year; the contribution was especially strong around October (the beginning of the major mosquito season). Figure 5 also demonstrates that the observed mosquito population dynamics cannot be reproduced in the Ejersa model without the correct representation of the wind profile. A large contribution from the *MGPs* was found around June, which accounts for the important *Anopheles* population dynamics during the secondary mosquito season.

The magnitude of the contribution of the environmental factors to the *Anopheles* population is summarized in Figure 6a, where the total number of simulated *Anopheles* mosquitoes are presented relative to those in the Ejersa model. The contributions of *temp, rh*, and *RFPs* were found to be small. Figures 5 and 6a reveal
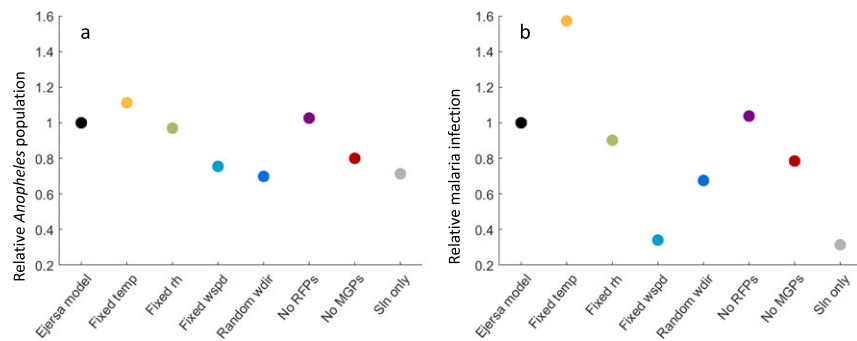
Figure 6. Simulated relative size of the *Anopheles* population and of malaria infections in investigation of the effects of environmental factors. Based on the Ejersa model, the contributions of environmental factors on the size of the (a) *Anopheles* population and of the (b) malaria infections are evaluated. The relative size of the simulated *Anopheles* population and malaria infections in each model is shown with respect to that in the Ejersa model (shown as 1 in black). Colors correspond to those in Figure 5.

the importance of the wind profile, both *wspd* and *wdir*. Large deviations from the Ejersa model were simulated both in the fixed *wspd* model and in the random *wdir* model. The simulated magnitude of the *Anopheles* population was 25% and 30% smaller than the Ejersa model in the fixed *wspd* model and in the random *wdir* model, respectively (Figure 6a). The wind profile was found to be an important factor dictating the dynamics and magnitude of the *Anopheles* population, and hence determining the risks of malaria transmission.

Similarly, the magnitude of the contribution of the environmental factors to malaria transmission is presented in Figure 6b. The total number of simulated malaria infections in each model relative to that in the Ejersa model is plotted. *Wspd* and *wdir* were also found to have significant contributions to malaria transmission. Although the impact of temperature was not significant for the *Anopheles* population (Figures 5 and 6a), it was of significant importance for malaria transmission (Figure 6b). While the increase in the *Anopheles* population was merely about 10%, the number of malaria infections increased by about 60%. Within the temperature range in Ejersa (19–24°C), the expected longevity of *Anopheles* is not sensitive to temperature. However, increase in temperature can significantly shorten the EIP, enhancing malaria transmission. With the fixed *temp* model, temperature during the major mosquito season (September–December) was higher than the observational values in the Ejersa model. The combination of the large *Anopheles* population and the higher temperatures resulted in a large number of malaria infections. Markedly, the result suggests the importance of the combined seasonal environmental factors.
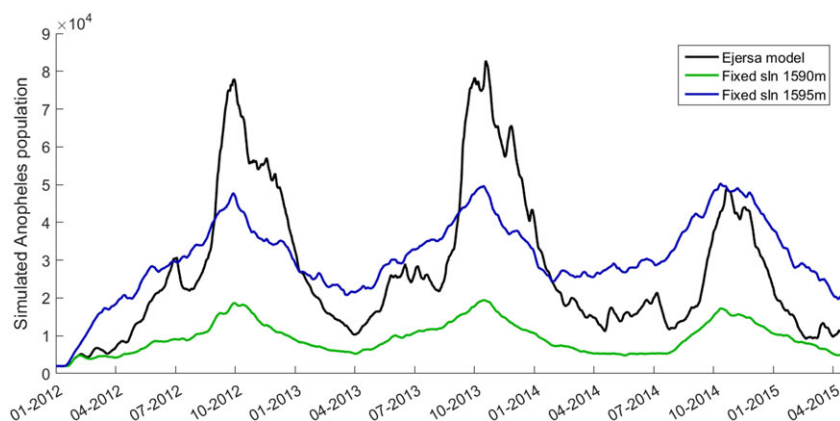

Figure 7. Simulated time series of the *Anopheles* population in investigation of the effect of shoreline locations. Two fixed *sln* models simulate the contributions of climatological factors by fixing the location of shoreline and removing the *RFPs* and the *MGPs*. One model used the shoreline corresponding to the reservoir water level of 1,590 masl (green) and another of 1,595 masl (blue). Remaining dynamics in *Anopheles* population should be explained solely by climatological factors. The result from the Ejersa model was shown in black.
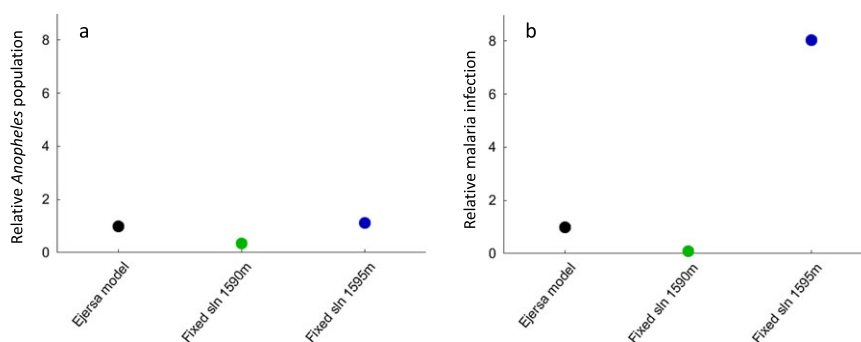
Figure 8. Simulated relative size of the *Anopheles* population and of malaria infections in investigation of the effect of shoreline locations. Based on the Ejersa model, the contributions of environmental factors on the size of the (a) *Anopheles* population and of the (b) malaria infections are evaluated. The relative size of the simulated *Anopheles* population and malaria infections in each model is shown with respect to that in the Ejersa model (shown as 1 in black). Colors correspond to those in Figure 7.

3.2. Impact of Shoreline Locations

Another set of two simulations was conducted fixing the locations of the shoreline and removing the *RFPs* and the *MGPs* (fixed *sln* model). One model used the shoreline corresponding to the reservoir water level of 1,590 masl (close to the observed minimum) and another of 1,595 masl (close to the observed maximum). The simulated time series of the *Anopheles* population in the two models are presented in Figure 7 in blue and green, respectively, and compared with those from the Ejersa model (black). Because there is no variability in the presence of breeding pools, the simulated dynamics in *Anopheles* population should be explained solely by the climatological factors. The magnitude of the simulated *Anopheles* population and malaria infection is summarized in Figure 8. These models further assert that the population dynamics of *Anopheles* mosquitoes in Ejersa arise from both the variability in climate factors and from the change in shoreline locations (gray line in Figure 5), but not merely from the existence of a reservoir.

4. Discussion

4.1. Three Environmental Mechanisms of Malaria Transmission Around the Koka Reservoir

The presented series of experiments elucidate a few important environmental mechanisms of malaria transmission around reservoirs. First, for *Anopheles* population dynamics, which of course affect the dynamics of malaria transmission, the wind conditions (both wind speed and wind direction) play a noticeable role. The effect of wind on the *Anopheles* population dynamics has received limited attention in the scientific community, yet particularly significant effect has been demonstrated around reservoirs (Endo & Eltahir, 2018). In reservoirs, as compared to those in small-scale puddles, larvae are more susceptible to mortality caused by wind-induced waves. Waves in reservoirs are generally higher than in small-scale puddles because the height of the wave increases with the depth and the fetch (fetch is defined as the length of water over which the wind blows in a single direction; fetch is thus a function of the size of a reservoir and wind direction) of a water body. In addition, the heterogeneity around reservoirs, where human settlements are located on one side and reservoir on the other side, makes the population dynamics of *Anopheles* mosquitoes sensitive to the wind direction. This high sensitivity of malaria transmission potential to wind direction around reservoirs suggests that malaria may be mitigated if villages are located around reservoirs in places where wind conditions are unfavorable for the reproduction of *Anopheles* mosquitoes.

Second, the distances to the shoreline from human settlements influence the *Anopheles* population dynamics. With the increase in reservoir water levels, the reservoir shoreline becomes closer to the village, making mosquito reproduction and malaria transmission more likely. The increase in water levels lags rainy seasons; and hence in Ejersa, the *Anopheles* seasons were observed to lag the rainy seasons by a few months. In water-limiting environments, it is also typically observed that *Anopheles* seasons follow rainy seasons. However similar these observations are, one should not confuse the distinctive mechanisms of the *Anopheles* population dynamics. At reservoir sites, where water is abundant throughout year, the mosquito population dynamics can be led by the shift in reservoir shorelines, which is a delayed response to the rainfall. Pools created by rainfall are not likely to play an important role in the mosquito population dynamics where water is already not limiting. On the other hand, in water-limiting environments, rainfall directly leads to the increase

in mosquito population through the creation of breeding puddles. Due to such difference, the lag between rainy seasons and mosquito seasons is larger at reservoir sites as compared to water-limiting sites. For example, in Niger, for which HYDREMATS was originally developed, the observed lag between the rainy season and the mosquito season was only about a month (Bomblies et al., 2008). In Ejersa, near the Koka Reservoir in Ethiopia, the observed mosquito season from September to December lagged the rainy season of July to September. Demonstrated impact of distance between a village and a shoreline on malaria transmission provides implication that a village should be located far enough from a reservoir to prevent malaria.

Finally, temperature was found to play an important role, not so much in *Anopheles* population dynamics, but in malaria transmission dynamics. In Ejersa, where the annual temperature is around 21°C, the increase in temperature does not affect mosquitoes' longevity significantly, but it amplifies the chance of malaria transmission through shortening the EIP. This result suggests a large sensitivity to temperature of malaria transmission at the temperature range in Ejersa. It may hint that warming trend of temperature could adversely impact the regions around Ejersa.

4.2. Explanation of Observed Seasonality in *Anopheles* Population and Malaria Transmission Dynamics in Ejersa

The major mosquito season corresponds to the period of high reservoir water levels, from September to December (Figures 3f and S5). The above experiments also demonstrate that the *Anopheles* population dynamics in Ejersa are largely caused by the seasonality in the location of reservoir shorelines (gray line in Figure 5). With the increase of the reservoir water levels, the area of the reservoir expands. At the scale of our simulation, high reservoir water levels do not significantly increase the area of the breeding site; however, with the increase of the reservoir water level, the reservoir shoreline becomes closer to the village. *Anopheles* use only the shoreline of reservoirs as breeding sites, but not the whole reservoir area. The Koka Reservoir changes its water levels by approximately 6 m annually from 1,589.5 masl to 1,595.5 masl (Figure 3f), which corresponds to about 0.3 to 1.2 km of the change in shoreline depending on location (Figure 2). The proximity of vector breeding pools to human habitats is an important factor both in increasing the abundance of mosquitoes and malaria transmission (Bomblies, 2014; Cano et al., 2006; Endo & Eltahir, 2016; Gu et al., 2006; Minakawa et al., 1999, 2002; van der Hoek et al., 2003). Both mosquitoes' reproductive activities and malaria transmission require mosquitoes to encounter breeding pools and humans. With mosquitoes' limited lifespan, having the shoreline breeding site closer to human habitats can significantly increase the abundance of *Anopheles* mosquitoes and the transmission of malaria, through enhancing the host-seeking and breeding efficiency.

The observed *Anopheles* population during the major mosquito season was smaller in 2014 than in 2012 and 2013 (Figure S5). From the middle of September to the end of December (14 surveys each year), the total numbers of *Anopheles* collected were 2,164; 1,863; and 1,581, respectively, in 2012, 2013, and 2014. In 2012 and 2013, the maximum reservoir water level reached 1,595.5 masl; however, in 2014, it was 1 m lower (Figure 3f). The reservoir water levels were constantly lower from July to December in 2014 than in the corresponding months of the previous two years, keeping the shoreline breeding sites farther away. Meteorological conditions in 2014 were similar to those in 2012 and 2013. The simulation result also confirmed the smaller *Anopheles* population during the major mosquito season.

The minor mosquito season occurs from April to June in Ejersa (Figure S5). An increase in the *Anopheles* population during this season was observed in 2013, though not in 2014 (no observation data available for 2012) (Figures S5, S8b, and S8c). This increase is likely to be due to the existence of marginal pools (maroon area in Figure S7) and the favorable wind profile for the mosquitoes' reproduction (light blue and blue areas in Figure S7). During this season, the reservoir water levels are at the annual minimum (Figure 3f) and the rainfall amount is not large enough to form persistent rain-fed pools (Figure 3e). Thus, the increase in population is not attributable to the closer proximity of shoreline breeding pools nor to abundant rain-fed pools. The increase in the *Anopheles* population during this season can partly be explained by the existence of marginal pools. Factors leading to the formation of marginal pools are as follows: rough soil surface, high capillary fringe, and high groundwater table, which are the characteristics of this season (Endo, 2017). Rainfall during this season also helps create marginal pools. Accordingly, marginal pools were simulated and contribute to *Anopheles* population dynamics between April and August (Figure S7). However, the formation of marginal pools alone cannot explain the observed difference between the minor mosquito seasons in 2013 (increase in *Anopheles* population observed) and the minor mosquito season in 2014 (increase in *Anopheles* population

not observed). Our analysis revealed that this difference is likely caused by the difference in wind direction. Figures 5 and S8 demonstrate that the observed wind direction in the minor mosquito season in 2014 worked to suppress the mosquito population (Figures 5 and S8f, black), as compared to an assumed condition with random wind direction (Figures 5 and S8f, blue). The observed wind direction in the minor mosquito seasons in 2012 and 2013 (Figures 5, S8d, and S8e, black), on the other hand, worked to enhance mosquito population slightly, as compared to an assumed condition with random wind direction (Figures 5, S8d, and S8e, blue). Thus, the minor mosquito season was found to be supported by both marginal pools and favorable wind direction.

Despite a smaller increase in *Anopheles* population during the minor mosquito season, the importance of this season on malaria transmission should not be neglected. The daily temperature during the minor mosquito season is around 23°C, 3° higher than that of the major mosquito season (Figure 3a). Around this range of temperature, a small increase in temperature enhances malaria transmission potential significantly. For example, with a temperature increase from 20 to 23°C, the EIP reduces from 27.8 days to 15.9 days for *Pf* and from 19.1 days to 12.4 days for *Pv* (Endo & Eltahir, 2016; Paaijmans et al., 2009). The importance of the minor mosquito season on malaria transmission is also demonstrated in the data on observed malaria cases (Figure S6).

The role of rain-fed pools in malaria transmission was found negligible. During the main rainy season from July to September, rain-fed pools rarely persisted long enough for *Anopheles* to complete its aquatic-stage development. At Ejersa, the temperature during the main rainy season is around 19.5°C, and the aquatic-stage development cycle takes about 15 days (Lautze et al., 2007). The persistence of rain-fed pools is determined by many factors, such as rainfall, topography, and soil type. In 2012, the amount of rainfall during the main rainy season was 800 mm, while those in 2013 and 2014 were 413 mm and 459 mm, respectively. Rain-fed pools were simulated to persist barely long enough only in 2012, but not in 2013 and 2014. Our surveys of breeding pools and larval abundance have confirmed that, at Ejersa, rain-fed pools are not as important as shoreline pools for most of the year because of their limited presence and persistence.

5. Conclusion

Dams and reservoirs are associated with exacerbated risk of malaria transmission; however, the *existence* of reservoirs is not the only factor to dictate the risk of malaria transmission. It was demonstrated that the distance between a shoreline and a village influences significantly the transmission potential of malaria, even at the intraannual scale because of the fluctuation of reservoir water levels. A strong contribution of wind profile to malaria transmission suggests that some sides of a reservoir will encounter smaller risk of malaria than other sides. These findings may provide suggestions to the locations of villages upon construction of resettlement villages.

Around the Koka Reservoir, variation in temperature does not influence *Anopheles* populations significantly, but its impact on malaria transmission is substantial. This result suggests that the seasonality of malaria transmission cannot necessarily be interpreted from the size of *Anopheles* populations and that the trend of warming in temperature is likely to exacerbate malaria in this region in the future.

Understanding the environmental mechanisms of malaria transmission elucidates environmental factors that can be controlled to suppress malaria, and thus informs efforts toward and prevention of malaria transmission. Combining extensive multiyear field surveys, rigorous model development, and simulation studies, this study describes detailed environmental mechanisms of malaria transmission that are important around reservoirs.

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