

Original Contribution

The Impacts of Land Use Change on Malaria Vector Abundance in a Water-Limited, Highland Region of Ethiopia

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Abstract: Changes in land use and climate are expected to alter the risk of malaria transmission in areas where rainfall limits vector abundance. We use a coupled hydrology–entomology model to investigate the effects of land use change on hydrological processes impacting mosquito abundance in a highland village of Ethiopia. Land use affects partitioning of rainfall into infiltration and runoff that reaches small-scale topographic depressions, which constitute the primary breeding habitat of *Anopheles arabiensis* mosquitoes. A physically based hydrology model isolates hydrological mechanisms by which land use impacts pool formation and persistence, and an agent-based entomology model evaluates the response of mosquito populations. This approach reproduced observed interannual variability in mosquito abundance between the 2009 and 2010 wet seasons. Several scenarios of land cover were then evaluated using the calibrated, field-validated model. Model results show variation in pool persistence and depth, as well as in mosquito abundance, due to land use changes alone. The model showed particular sensitivity to surface roughness, but also to root zone uptake. Scenarios in which land use was modified from agriculture to forest generally resulted in lowest mosquito abundance predictions; classification of the entire domain as rainforest produced a 34% decrease in abundance compared to 2010 results. This study also showed that in addition to vegetation type, spatial proximity of land use change to habitat locations has an impact on mosquito abundance. This modeling approach can be applied to assess impacts of climate and land use conditions that fall outside of the range of previously observed variability.

Keywords: land use change, root uptake, overland flow, hydrology model, malaria, *Anopheles gambiae*

INTRODUCTION

Background

Despite overall decreases in worldwide cases of malaria (World Health Organization 2009), in highland regions of Africa malaria epidemics have recently escalated (Lindsay and Martens 1998). Most cases of malaria in Africa, including those in highland regions, are caused by the

protozoan parasite *Plasmodium falciparum* (Patz et al. 1998), which is transmitted to humans by the *Anopheles* mosquito (Beier 1998). Lower temperatures have a limiting effect on the sporogonic development of the main malaria parasite, so highland areas where average temperature is below a threshold are often malaria free. Highland regions that do experience malaria see short transmission seasons and long intervals between transmission periods (Abeku et al. 2003), thereby resulting in human populations with low acquired immunity which suffer especially high rates of morbidity and mortality as a result of epidemics (Lindsay

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and Martens 1998; Kiszewski and Teklehaimanot 2004). Highland regions in Ethiopia suffered large-scale epidemics in 1953 and 1958, during which 7,000 and 150,000 deaths were attributed to malaria, respectively (Fontaine et al. 1961). The sensitivity to environmental variability and potentially severe nature of malaria risk make highland areas a valuable site for investigating the impacts of specific processes affecting vector mosquito population dynamics. We apply this modeling study to a highland area in Ethiopia where malaria occurs seasonally and epidemically.

Climate and Environmental Drivers of Malaria Transmission

Previous studies have correlated environmental variables, such as temperature and rainfall, with changes in vector populations and malaria occurrence (Odongo-Aginya et al. 2005; Briët et al. 2008). The 1953 epidemic in Ethiopia was associated with unusually high rainfall over an extended period, as well as with elevated temperatures and relative humidity (Fontaine et al. 1961). Temperature has one of the most recognized influences on transmission of malaria through its effects on the development of the mosquito vector and malaria parasite (Craig et al. 1999; Depinay et al. 2004; Detinova 1962; Lindsay and Martens 1998). The length of the extrinsic incubation period and daily survival rate of the mosquito depend on ambient temperatures, so that a relationship exists between temperature and the percentage of a vector cohort that survives long enough for the malaria parasite to complete sporogony (Craig et al. 1999). If sporogonic development is longer than the lifespan of mosquitoes, malaria transmission will not occur (Onori and Grab 1980; Detinova 1962).

Land use has also been investigated as a driver of changes in mosquito population dynamics. In Kenya, deforestation has been shown to cause local increases in temperature and humidity, altering the development and densities of local vector populations (Afrane et al. 2008; Minakawa et al. 2005; Yasuoko and Levins 2007). Cumulative deforestation in Brazilian health districts was linked to statistically significant increases in malaria incidence (Olson et al. 2010). Cultivated swamps in Uganda have been shown to have higher temperatures, higher mosquito densities, and higher malaria transmission than natural swamps (Lindblade et al. 2000). Higher temperatures and nutrient levels in farmland habitats have also been shown to favor *Anopheles gambiae* larval survival and productivity (Munga et al. 2006). Ye-Ebiyo et al. (2003) showed that

proximity to flowering maize could exacerbate local malaria transmission due to increased vector longevity arising from high levels of nutriment (maize pollen) available to mosquito larvae.

One potentially important effect that has not been adequately investigated is the role of hydrological processes associated with land use in mosquito population dynamics. Changes in land cover affect land surface energy and water balances (Hutjesa et al. 1998; Bonan et al. 2005), by altering physical parameters that influence small-scale hydrology and microclimate. For instance, plant canopy properties affect processes such as evapotranspiration and soil moisture, which regulates infiltration and runoff. Surface roughness is affected by vegetation structure and affects momentum and movement of heat (Bonan et al. 2005; Hutjesa et al. 1998). Vegetation has a critical role in determining rainfall partitioning (Gordon et al. 2003), and is one of the primary determinants of runoff (Cerdeira 1999; Freebairn and Wockner 1986). In environments where water availability limits mosquito reproduction, runoff can be a dominant mechanism by which temporary pools form in topographical depressions, creating the majority of productive *A. gambiae* breeding habitats (Bombliès et al. 2008; Gimnig et al. 2001; Minakawa et al. 1999, 2005). This study investigates the hydrologic link between land use and changes in mosquito abundance, through the formation and persistence of vector breeding habitats.

Mathematical models have previously been used to predict local hydrological conditions that contribute to the abundance of mosquito vectors and malaria transmission. Patz et al. (1998) used a physically based soil moisture model to improve correlative predictions of abundance and human biting rates of *A. gambiae* in western Kenya. Shaman et al. (2006) used a mosquito life cycle model linked to a hydrology model to incorporate effects of temperature on developmental rates and habitat availability. Results showed an increase in abundance of *Anopheles walkeri* mosquitoes with warmer temperatures and increased surface wetness (Shaman et al. 2006). Here, we use numerical models to isolate processes affecting runoff generation and evaluate the response in mosquito abundance to variability in pool persistence caused by land use change. We expect that increasing vegetation that utilizes more water (such as rainforest) will decrease water available for pooling, thereby decreasing mosquito abundance. Conversely, an increase in surface runoff and mosquito abundance is expected in response to increasing areas of vegetation such as agriculture.

METHODS

Hydrology Model

The hydrology model is described in Bombliet et al. (2008), so here we specifically address hydrologic processes and associated parameters that vary with land use and affect the presence of surface waters exploited by Anopheles mosquitoes. In particular, we consider the sensitivity of ephemeral pool persistence to Manning's n , leaf area index (LAI), and Jackson's rooting parameter (β). Hortonian overland flow, directed by microtopography, is treated as the main determinant of pool formation in this study. Horton (1933) described the process by which water in excess of soil infiltration capacity, flows horizontally over the land surface and so is available to fill topographical depressions. Overland flow as a result of saturation from below (Dunne and Black 1970a, b) is not represented here; due to groundwater and soil characteristics this is not expected to significantly affect results. Significant hydrological mechanisms contributing to pool formation in the hydrology model are illustrated in Fig. 1.

Distributed flow routing is calculated using an implicit finite difference solution to the St. Venant equations (equations for shallow water flow), at each one second time step. Manning's equation is used to relate shallow flow velocity to flow depth, slope, and friction or roughness of

the land surface. For the x direction, flow velocity is described by Manning's equation:

$$u = \frac{1}{n} h^{2/3} S_f^{1/2} \quad (1)$$

where u is the flow velocity in the x direction, h is the water depth, S_f is the friction slope (in the x direction), and n represents surface roughness and determines resistance to overland flow. The y direction velocity is formulated similarly. Higher values of Manning's n indicate increased resistance to overland flow, so it is expected that higher values of n correlate with more time for water to infiltrate prior to reaching topographic low points, and thereby less pooling. Smaller values of n are expected to increase the persistence of temporary pools. Generally, smaller, more tightly spaced plant stalks provide more resistance to overland flow.

Water that infiltrates the soil gets distributed in the unsaturated zone, where vertical movement is determined using Richard's equation (Richards 1931). Plant properties influence the uptake of water, a key element determining soil moisture, which affects rainfall partitioning and runoff generation (Feddes et al. 2001; Jackson et al. 2000). Here, the root system is modeled as a sink present in each soil layer (Feddes et al. 2001). This method does not incorporate lateral water transfer, so it must be used with careful consideration in the case of sloping groundwater tables and

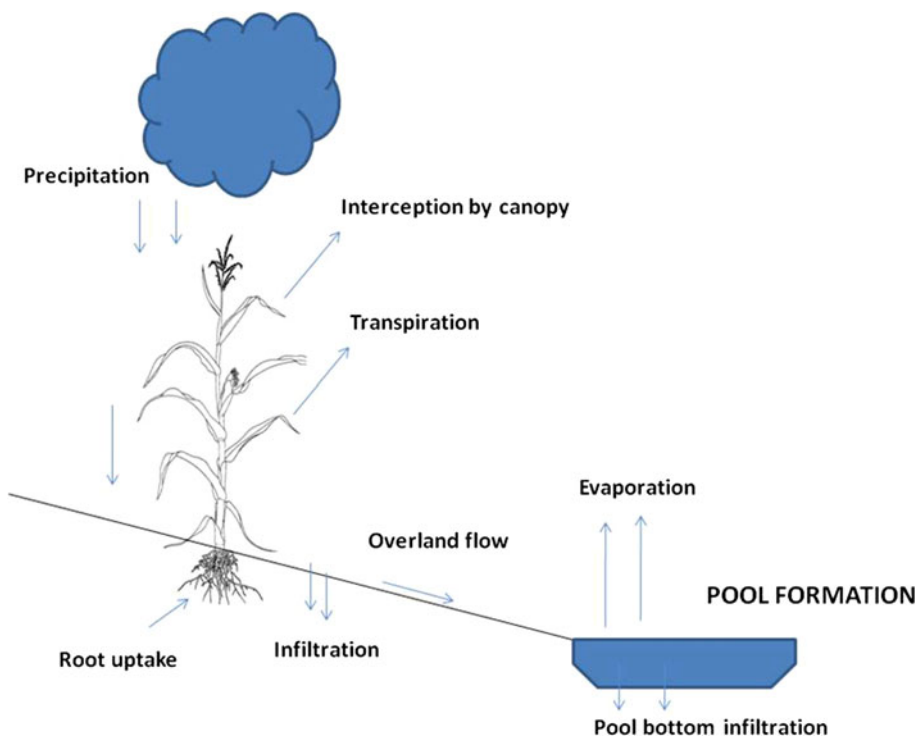


Fig. 1. Modeled hydrological mechanisms contributing to pool formation and persistence.

terrain. The sink term incorporating plant root uptake is added to Richard's equation:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[K(\psi) \left(\frac{\partial \psi}{\partial z} + 1 \right) \right] - S(z), \quad (2)$$

where θ is the volumetric water content, K is the hydraulic conductivity, and S is the actual root water uptake rate ($\text{cm}^3 \text{cm}^{-3} \text{day}^{-1}$).

The effects of vegetation on water uptake are incorporated in the sink term for each soil layer as:

$$S_i = PF_i, \quad (3)$$

where S is the water uptake in that soil layer (m s^{-1}), P is the plant transpiration (m s^{-1}), and F is the fraction of water uptake in that layer. Transpiration fluxes from unit leaf area are determined using climate variables and plant canopy properties, including LAI. A detailed description of this mechanism is provided by Pollard and Thompson (1995), and equations for these fluxes can also be found in Li et al. (2005). Greater LAI values are expected to increase transpiration and root zone uptake (Chase et al. 1996), reducing soil moisture, decreasing runoff, and shortening persistence of nearby ephemeral pools. The converse would also be expected for a reduction in LAI.

The fraction of water uptake in each soil layer (F_i) is based on the fraction of root biomass and soil water availability of each layer (Li et al. 2005). The root biomass component of the calculated water uptake is found by

$$R_i = Y_i - Y_{i-1}, \quad (4)$$

where Y is the cumulative fraction of roots reaching each soil layer from the ground surface. This cumulative root fraction is represented by an asymptotic equation:

$$Y=1 - \beta^d, \quad (5)$$

where d is the depth from soil surface, and β is an estimated parameter that provides a numerical indicator of rooting distribution (Jackson et al. 1996; Jackson et al. 1997; Gale and Grigal 1987). Jackson's parameter, β , has been determined for many vegetation types by assimilating studies on root properties such as fine/total root biomass, root length, maximum rooting depth, root/shoot ratio, and nutrient content (Jackson et al. 1996; Jackson et al. 1997). Equation 5 describes the decreasing proportion of roots with increasing soil depth, where lower values of β correspond to a larger portion of roots at shallower depths. It is expected that lower β values represent more water uptake by plants in shallow soil layers and results in drier near surface soil moisture conditions.

Entomology Model

The entomology model was developed by Bomblies et al. (2008), and is used here with no methodological modifications. Water temperature, air temperature, humidity, wind speed and direction, as well as distributed water depth outputs of the hydrology model, are provided as real-time hourly inputs. Based on the simulated persistence of water in any grid cell, mosquito larvae develop through several developmental stages including eggs, four larval stages, pupae, and then adult emergence. If a pool dries out in the hydrology model, larvae within that pool die in the entomology model. When the pool reforms, aquatic stage development begins anew in those grid cells where water exists, if a gravid mosquito lays eggs there.

Once mosquitoes emerge, a set of characteristics including location, time since emergence, blood meals, and egg-laying, are tracked for each adult mosquito and updated at each time step. Individuals fly in a radial random walk in which behaviors depend on proximity of each mosquito to features of the physical environment. Flight velocity is a calibration parameter and is adjusted to reflect dispersal comparable to that found by Costantini et al. (1996) near Burkina Faso. A cycle of host seeking, biting, resting, oviposition, and again host seeking, repeats until death of the mosquito. A set of rules guide specific events such as oviposition and blood meals, which in addition to dispersal behaviors, are determined by probability density functions. Probabilistic adult mortality at each time step is represented by a daily survivability factor according to Martens et al. (1997)

$$p = \exp\left(\frac{-1}{-44 + 1.31T_d - 0.03T_d^2}\right), \quad (6)$$

where p is the daily survivability probability for each mosquito, and T_d is the average temperature of the last 24-h period. In addition, local residents are incorporated in the model as immobile and individual humans based on the observation that *A. gambiae* mosquitoes primarily seek blood meals from humans, between dusk and dawn when people are typically in their houses (Service 1993).

Study Site

This study was conducted in Waktola, a village in Omo Nada woreda, Jimma zone, Oromia region of Ethiopia (7.7°N, 37.2°E, 1,750 m a.s.l.). Approximate location of Waktola is indicated in Fig. 2. Most of the population



Fig. 2. Location of field site; Waktola, Ethiopia.

depends on subsistence farming and consequently most arable land is used for crops or as pasture. Crops consist largely of maize, as well as of teff, taro, red pepper, and others. A topographic low area exists near the center of Waktola and local elevation ranges from ~1,740 to 1,800 m a.s.l. The landscape is dotted with small topographical depressions (borrow pits) which are dug by residents harvesting the clayey soil for use in construction. Borrow pits range in size from several meters to several tens of meters in diameter. During rain events, pits fill with water and form the principal breeding habitat of *Anopheles arabiensis* mosquitoes. Examples of water-filled borrow pits at the site are shown in Fig. 3. This habitat offers mosquitoes shallow, turbid, and ephemeral water for breeding, and is consistent with observations of *Anopheles* breeding



Fig. 3. Examples of pooled water forming *Anopheles gambiae* breeding habitats in Waktola, Ethiopia.

Table 1. Comparison of Measured Climate Variables During 2009 and 2010 Wet Seasons

	2009 (July 2nd– October 31st)	2010 (July 2nd– October 31st)	2010 (May 1st– October 31st)
Average temperature (°C)	18.2	17.9	18.4
Maximum temperature (°C)	28.9	29.0	29.3
Minimum temperature (°C)	7.1	7.2	7.2
Average humidity (%)	83.9	85.1	84.4

from other studies (Bomblies et al. 2008; Minakawa et al. 1999, 2004). Waktola experiences seasonal and epidemic malaria typical of the region, accounting for ~77% of all reported disease in 2006 and 2007 (Assefa et al. 2010).

Field Measurements

We installed a meteorological station onsite that records temperature, relative humidity, precipitation, wind speed/direction, and net radiation every 15 min beginning in July 2009. Seasonal climate statistics for each wet season in Table 1 and Fig. 4 show cumulative 2009 and 2010 rainfall. Climate comparison and model runs were started on May 1st for 2010 scenarios and on July 2nd for 2009 runs, and ended October 31st. Field observations made by villagers and researchers present in the field indicated that little rainfall had occurred earlier than July 2009, whereas in

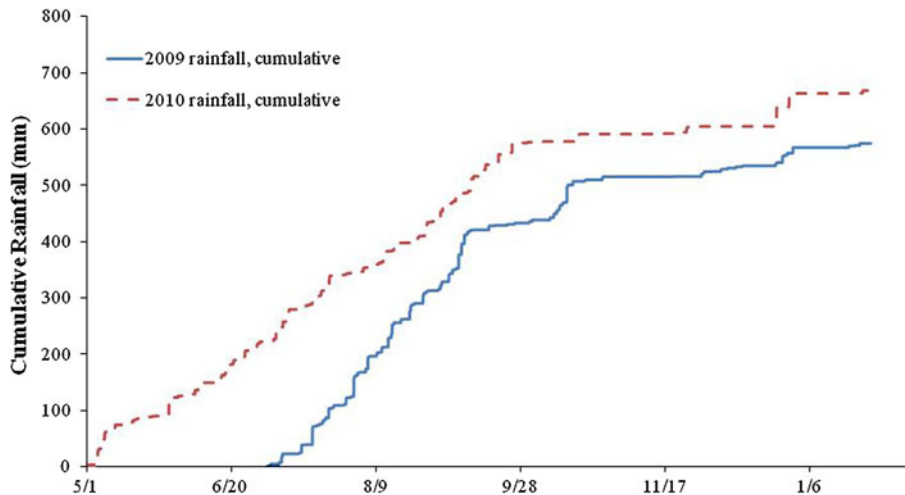


Fig. 4. Cumulative rainfall through the major wet and dry seasons of 2009 and 2010.

2010, the rains began in May. This difference was considered important in simulating a full season of mosquito population development, and meteorological data is not available earlier in 2009, so start dates reflect onset of rains in each season. Different model start dates produced plausible representations of mosquitoes present in the environment as of mid-July in both years, when light trap counts could be used to validate data; thus comparison of mosquito abundance begins July 15th. Earlier onset of rains in 2010 resulted in prolonged wet conditions and higher cumulative mosquito abundance through the season. More mosquitoes indicates higher breeding potential early in the 2010 season, whereas in 2009 an increase in mosquito abundance was seen only later in the season after rains had begun.

Time domain reflectometry (TDR) probes measured volumetric water content (VWC) at depths of 5, 20, 50, and 100 cm below the ground surface at five locations in the field. VWC was recorded every 30 min, also beginning in July 2009. Locations for soil monitoring were chosen so as to sample a range of soil types, and TDR probes were calibrated by conducting gravimetric tests. A known volume of soil was collected, weighed, oven dried, and re-weighed to obtain VWC at those locations. Field-conducted double-ring infiltrometer tests confirmed faster surface infiltration at higher elevations and decreased infiltration at lower elevations due to differences in permeability. Measured rates were consistent with literature-cited values of saturated hydraulic conductivity for clayey silt and clay soils (Freeze and Cherry 1979).

Water depth and surface area were observed regularly during the 2009 and 2010 wet seasons at locations where water repeatedly formed productive breeding habitats.

Submersible pressure transducers measured water depth of recurring pools every ten minutes at two locations. Center for Disease Control (CDC) light traps were used to collect mosquitoes at eight locations throughout the site. CDC traps were standard traps with battery-powered incandescent light bulbs and fans that prevent insects from escaping once in a collection bag. Four traps were placed within homes near family sleeping areas, and four were placed outside of dwellings near where animals were kept at night. Larval abundance was used to assess productivity of breeding habitats, and specific light trap locations were chosen based on proximity to productive pools as well as the willingness of residents to accommodate the devices. Light traps were set overnight and collected the following morning on a weekly schedule with dates adjusted for lunar phases. Mosquitoes were anesthetized, and were identified morphologically to species complex (Gillies and Coetzee 1987).

Model Domain and Inputs

The model domain was comprised of a 2.0 km by 2.0 km area encompassing all sample locations. The model domain was sized to include several productive breeding habitats as well as to roughly encompass *A. gambiae* mosquito flight distances, where typical flight distance from emergence location to blood meals over mosquito lifetime of *A. gambiae* is ~1 km (Costantini et al. 1996; Gillies and Wilkes 1965). 10-m grid cells were used in both models because they roughly encompass typical breeding pools. Figure 5 shows the model domain, locations of measured data, and other site information. Meteorological variables were entered in the model as hourly inputs, and assumed constant over the entire domain.

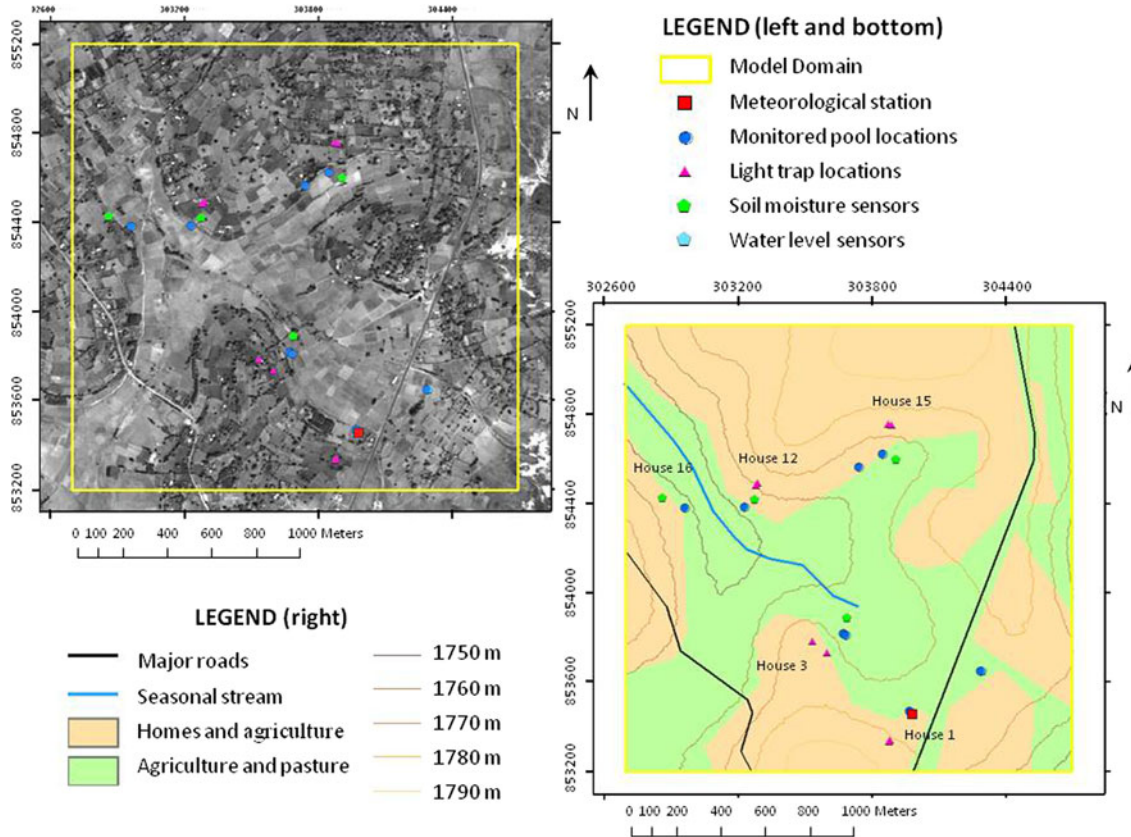


Fig. 5. WorldView-2 satellite image of study site and corresponding GIS map outlining model domain and locations of collected field data.

Topographical information was acquired using the three arc-seconds (~ 90 m) product from Shuttle Radar Topography Mission (SRTM) and interpolated to create a 10 m resolution digital elevation model (DEM). Individual cells were modified manually to represent depth of borrow pits as observed in the field. Borrow pits were considered the only significant small-scale topographic features capturing pooled surface water and affecting mosquito abundance by this mechanism, so this approach sufficiently captures relevant topographic characteristics of the site. Geographic information system (GIS)-derived raster maps of vegetation and soil distribution were also created using a 50-centimeter resolution image from the WorldView-2 satellite, based on ground truth from field observations. Land use was digitized and classified into categories including roads/homesteads with no vegetation, pasture, maize, cultivated peppers and other crops, and eucalyptus trees. For each cell, vegetation type dictates LAI, surface roughness (Manning's n), and β . Values of these parameters were chosen based on numerous studies (Chow 1959; Jackson et al. 1996, 1997; Asner et al. 2003; Myneni et al. 2002). Values are listed in Table 2. Soil distribution was also digitized and is shown in Fig. 6. Soil texture is desig-

nated as percent clay (as shown in Fig. 6). This value is not used in calculations, but assigns porosity, saturated hydraulic conductivity, and unsaturated zone retention parameters to each model grid cell. The areas designated as 99% clay represent recurring borrow pit locations where soil permeability was significantly decreased due to pore clogging from fine sediment accumulation, as in Desconnets et al. (1997). These areas were considered impermeable and are represented as such in the hydrology model.

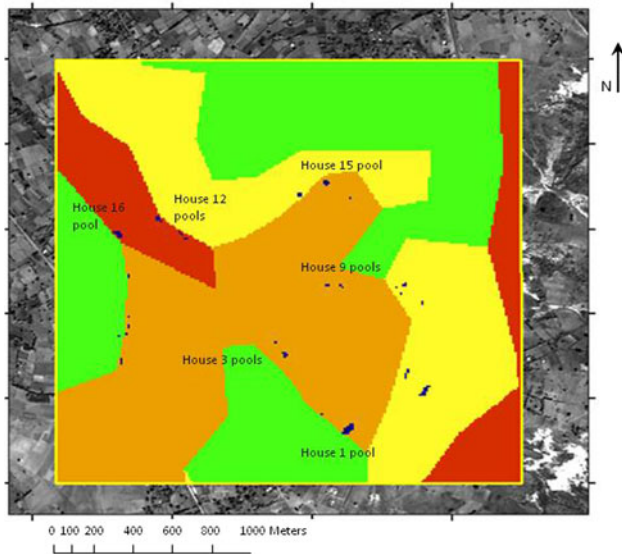
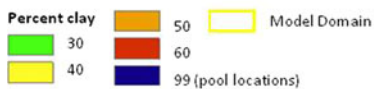
Model Calibration

Hydrology Parameters

VWC data from field measurements were used to fit model soil parameters including saturated hydraulic conductivity (K_s), porosity (θ_s), air entry potential (ψ_e), and Campbell's curve fitting exponent (b). Values for these parameters were initially chosen based on literature-cited values for soil types observed in the field (according to soil texture obtained from field tests), and afterwards adjusted to improve correlation of simulated and measured soil moisture variability through the

Table 2. Values of Parameters Describing Specific Vegetation Types

Vegetation type	Total leaf area index, LAI	Jackson's parameter, β	Roughness coefficient, n
Maize/grass crops	3.62	.961	0.06
Vegetative crops	1.65	.961	0.06
Teff	1.40	.966	0.30
Pasture	1.10	.942	0.20
Eucalyptus trees	4.80	.972	0.40
Rainforest	6.0	.982	0.65
Bare land/houses/dirt walkways	N/A	N/A	0.02
Paved road	N/A	N/A	0.01

LEGEND**Fig. 6.** Example of GIS raster layer with polygons describing soil type by percent clay, where 99% represents decreased permeability of pool bottoms.

2009 season. Each calibration parameter was tested individually to assess sensitivity, and then sets of parameters were tested for best fit. Results of calibration are discussed below.

Entomology Parameters

The entomology model was largely adapted for modeling *A. gambiae* population dynamics (Bomblies et al. 2008), such that few parameters required calibration. The

parameters for mosquito dispersal (flight velocity) and ecological carrying capacity were calibrated to fit relative change in modeled mosquito abundance between 2009 and 2010, to cumulative light trap catches of mosquitoes in the field. Ecological carrying capacity was used to constrain aquatic stage development as total biomass in a pool approaches a set value (Depinay et al. 2004). Breeding was disallowed in cells that comprised a seasonal stream, based on observations that water here moved too quickly and reached depths greater than those suitable for *Anopheles* larval development (Bomblies et al. 2008; Minakawa et al. 2005).

Mosquito abundance from July 15 to October 12 was used for comparison of observation to predictions, based on availability of light trap data for both years. The model's ability to reproduce the relative difference in mosquito abundance between 2009 and 2010 seasons was validated by comparing cumulative modeled abundance and cumulative time integrated light trap catches. Model results discussed below are mean results of ten identical model runs with different random seeds.

RESULTS**Calibration Results**

Calibration results from the 2009 hydrology model run were validated using 2010 VWC data. Modeled and measured VWC results for two locations are shown in Fig. 7. Correlation coefficient (R) and coefficient of determination (R^2) were calculated over the time period shown on graphs and are also indicated on Fig. 7. R^2 values for surface soil moisture (5 cm depth), at four locations with different soil types, ranged from 0.576 (in the deep layers) to 0.922 for the time period shown on plots. Final calibrated fit was significantly better at depths of 5 and 20 cm, when compared to 50 and 100 cm. This was likely due to lateral flow occurring in deeper layers, especially on slopes, which was not represented by the hydrology model. Modeled and measured pool depth was also used to support model validation; this data is shown in Fig. 8. Pool depth at House 9 was monitored continuously, while at other locations discrete weekly measurements were made during the 2010 season. Modeled depth corresponds adequately with observed pool depth, although there were some differences that may in part be due to changing bathymetry of pool bottoms.

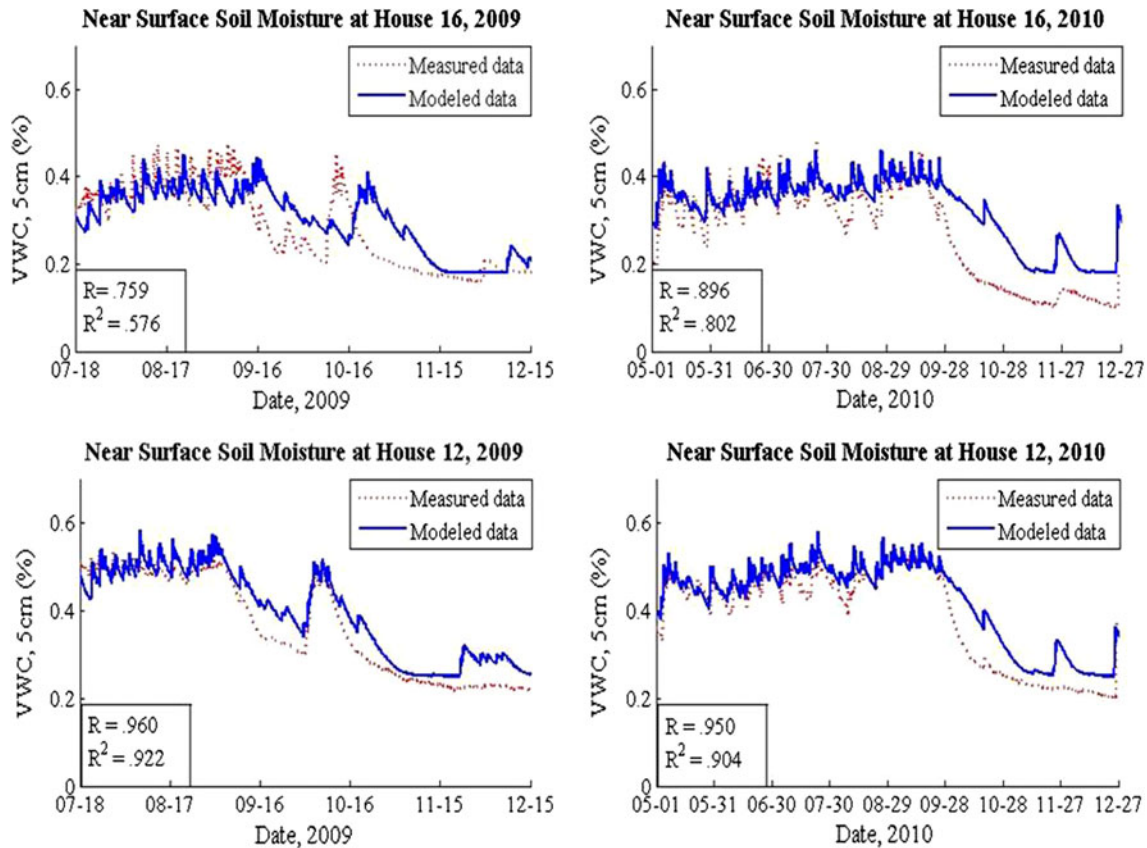


Fig. 7. Measured versus modeled near surface soil moisture values, in % volumetric water content (VWC), for 2009 and 2010 wet seasons for two soil types, as well as corresponding R^2 values.

Light traps indicate a 39% increase in cumulative mosquito abundance between 2009 and 2010 seasons. The calibrated entomology model simulated a 52% increase. These relative differences in mosquito abundance are shown in Fig. 9 in which the left y axis indicates the cumulative number of mosquitoes found in light traps, the right y axis indicates the cumulative number of mosquitoes existing in the model at the same dates. The model does not capture the seasonal population dynamics very well in July and August. This may be due to an unknown process that is affecting the population and not included in the model. However, a significant factor contributing to the imperfect model representation of the relative difference in mosquito abundance is that CDC light traps provide a poor measure of absolute abundance. The area of a model cell in which a trap is located is not necessarily the same as the area of influence of a trap in the environment (Horsfall 1943; Bomblies et al. 2008). Due to this element of light trap usage, as well as other factors affecting light trap effectiveness (Service 1993; Mboera et al. 1998), the exact number of mosquitoes predicted for a cell and caught in a light trap was not expected to be the same. Axes on Fig. 9

are designed to exhibit the comparable difference in mosquito abundance between the two seasons, and not to show an exact match in population numbers. Results in Fig. 9 indicate general agreement with modeled results and the relative differences in cumulative mosquitoes as measured by the light traps. Unknown, non-simulated processes and limited sampling methodology notwithstanding, the relative abundances are suitably reproduced and the higher modeled abundance in 2010 despite lower rainfall over the same time period is notable. We consider the model sufficiently validated for sensitivity analysis of hydrological processes.

Mosquito Abundance in Scenario Runs

Performed model runs are listed in Table 3, and examples of land use scenarios are shown in Fig. 10. Results of scenario runs were compared to the 2010 baseline vegetation results, for the time period from June 1 to October 31. 2010 meteorological data was used for all scenarios, so as to hold climate effects constant (this was the only full season of meteorological data available for running scenarios).

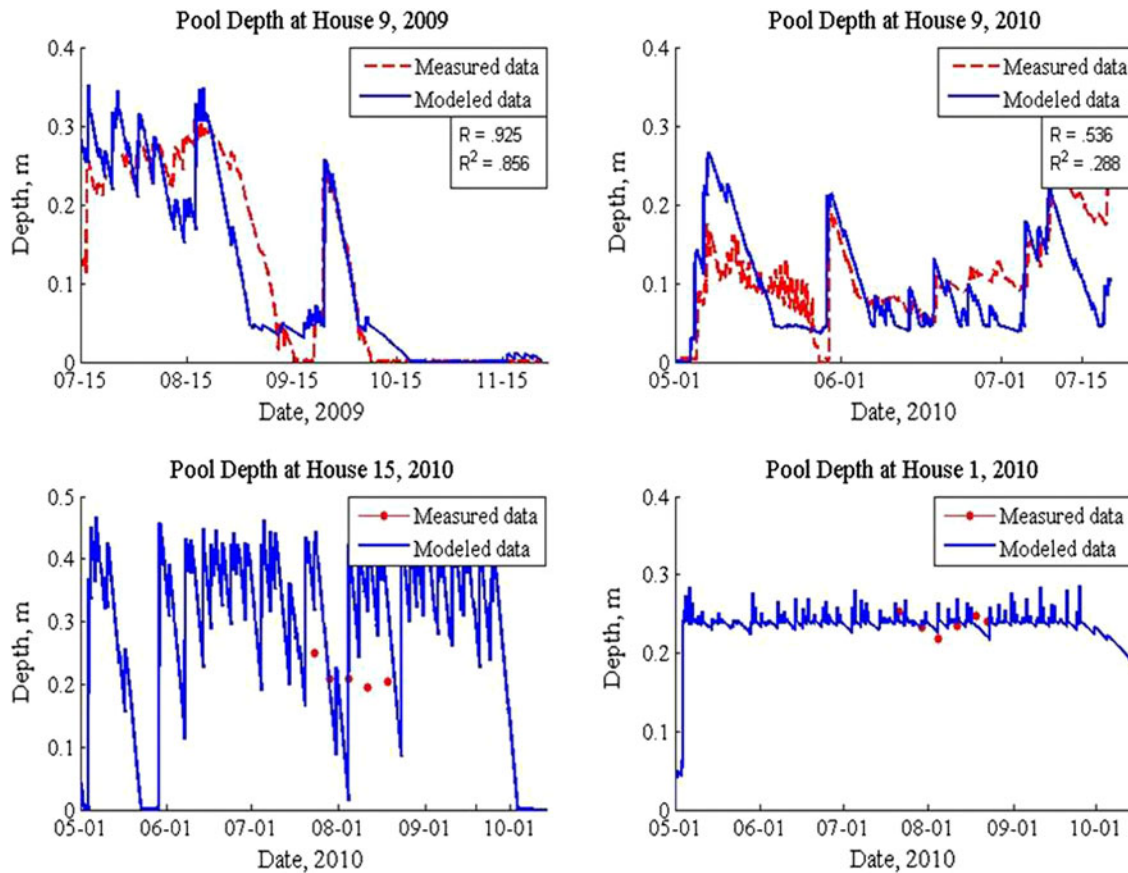


Fig. 8. Pool depth results and comparison to measured/field collected data, including R^2 values.

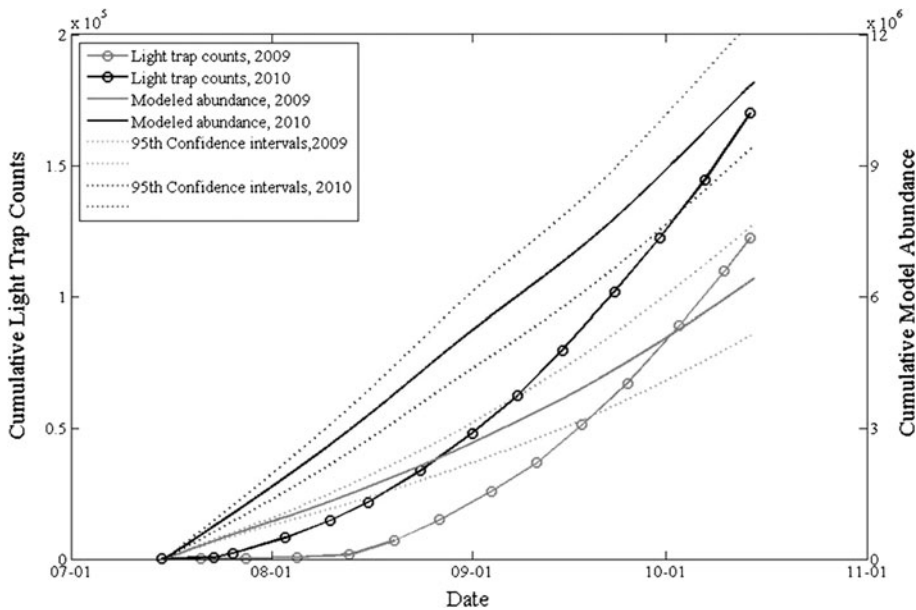


Fig. 9. Relative difference in cumulative mosquito abundance between 2009 and 2010 in light trap catches and modeled mosquito populations. *Left y axis* shows cumulative light trap counts and the *right y axis* shows model-generated cumulative mosquito abundance. *Dotted lines* indicate 95th percentile confidence intervals for 2009 and 2010 baseline scenarios, based on ten repeat runs.

Cumulative abundance at the end of the season (on October 31st) was used to smooth out short-term variability in mosquito abundance. Results are the mean of ten

repeated model realizations which were performed to assess internal model stochasticity, and 95th percentile confidence intervals were determined for each scenario. Results were

Table 3. Description of Vegetation Scenarios and Areas Modified, as a Percentage of Total Land Area Existing in Model Domain

Simulation	Location of areas modified	Percent pasture (%)	Percent maize (%)	Percent peppers (%)	Percent trees (%)	Percent teff (%)	Percent rainforest (%)	Scenario results (% change from baseline)
2009 Baseline	N/A	15.2	62.9	9.2	3.7	0	0	N/A
2010 Baseline	N/A	14.3	63.4	9.3	3.7	0	0	N/A
1: All maize	All	0	100	0	0	0	0	+10.1
2: All pasture	All	1,000	0	0	0	0	0	-25.8
3: All teff	All	0	0	0	0	100	0	-26.0
4: All peppers	All	0	0	100	0	0	0	+15.6
5: All trees	All	0	0	0	100	0	0	-27.9
6: All rainforest	All	0	0	0	0	0	100	-34.3
7: 25% to pasture	Random	40.6	38.4	9.3	3.7	0	0	-1.4
8: 25% to peppers	Random	14.3	38.4	34.3	3.7	0	0	+5.5
9: 25% to trees	Random	14.3	38.4	9.3	28.7	0	0	-10.6
10: 10% to trees	Adjacent of pools	24.3	53.5	9.3	3.7	0	0	-1.6
11: 10% to trees	Uphill to pools	24.3	53.5	9.3	3.7	0	0	-.6
12: 10% to pasture	Adjacent of pools	14.3	53.5	9.3	13.7	0	0	+10.3
13: 10% to pasture	Uphill to pools	14.3	53.5	9.3	13.7	0	0	+3.3

Last column of table shows results of scenario runs, where cumulative mosquito abundance in each scenario is compared to cumulative abundance in the 2010 baseline scenario.

generally consistent with the premise that lower Manning's n , higher LAI, and higher β would result in lower mosquito abundance, and that the converse would also be true.

Scenarios 1–6 were classified entirely as maize, peppers, teff, pasture, trees, and rainforest, respectively. Model simulations indicate an increase of 10.1 and 15.6% in mosquito abundance from Scenario 1 (maize) and Scenario 4 (peppers), respectively. The model shows a decrease of 25.8, 26.0, 27.9, and 34.3% in response to Scenario 2 (pasture), Scenarios 3 (teff), Scenario 5 (trees), and Scenario 6 (rainforest), respectively. In Scenarios 7–9, 25% of land cover was changed to pasture, peppers, and trees, respectively. Scenario 8 (increased peppers) produced a 5.5% increase in mosquito abundance, while Scenario 7 (increased pasture) and Scenario 9 (increased trees) produced a 1.4 and 10.6% increase, respectively. Scenarios 10 and 11, where 10% of land was modified from maize to trees, both adjacent to and uphill of pits, produced a 1.6% decrease and 0.6% increase in mosquito abundance, respectively. Scenario 12 and 13, where maize was transformed to pasture adjacent to and uphill of pool locations, resulted in a 10.3 and 3.3% increase, respectively. Results of all scenario runs, including confidence intervals, are shown in Fig. 11 and summarized in Table 3.

Baseline scenarios are dominated by land classified as agriculture, particularly maize. Maize and peppers were considered row crops, and were assigned the lowest values of Manning's n (peppers were also assigned a lower LAI value than maize). Pasture and teff had lower LAI values than maize, but higher resistance to overland flow. Trees and rainforest were assigned the highest values of Manning's n , as well as the highest values of LAI. Scenarios 1–9 indicate that vegetation types described by higher n and LAI values (such as trees and rainforest) generally reduce runoff and decrease mosquito abundance, while lower n and LAI values over more land area (such as with maize and peppers) increased abundance compared to the baseline scenario. In the case of Scenarios 10–13, although differences between mean cumulative abundance was small, it appears that higher n and LAI values resulted in somewhat lower mosquito abundances, particularly when changes were made close to pool locations.

Sensitivity runs were conducted to assess which parameters were most influential in affecting mosquito abundance. The 2010 baseline scenario was used for all following runs, and values of each parameter were separately increased and decreased by 10% for all vegetation types. Results of sensitivity runs are summarized in Table 4.

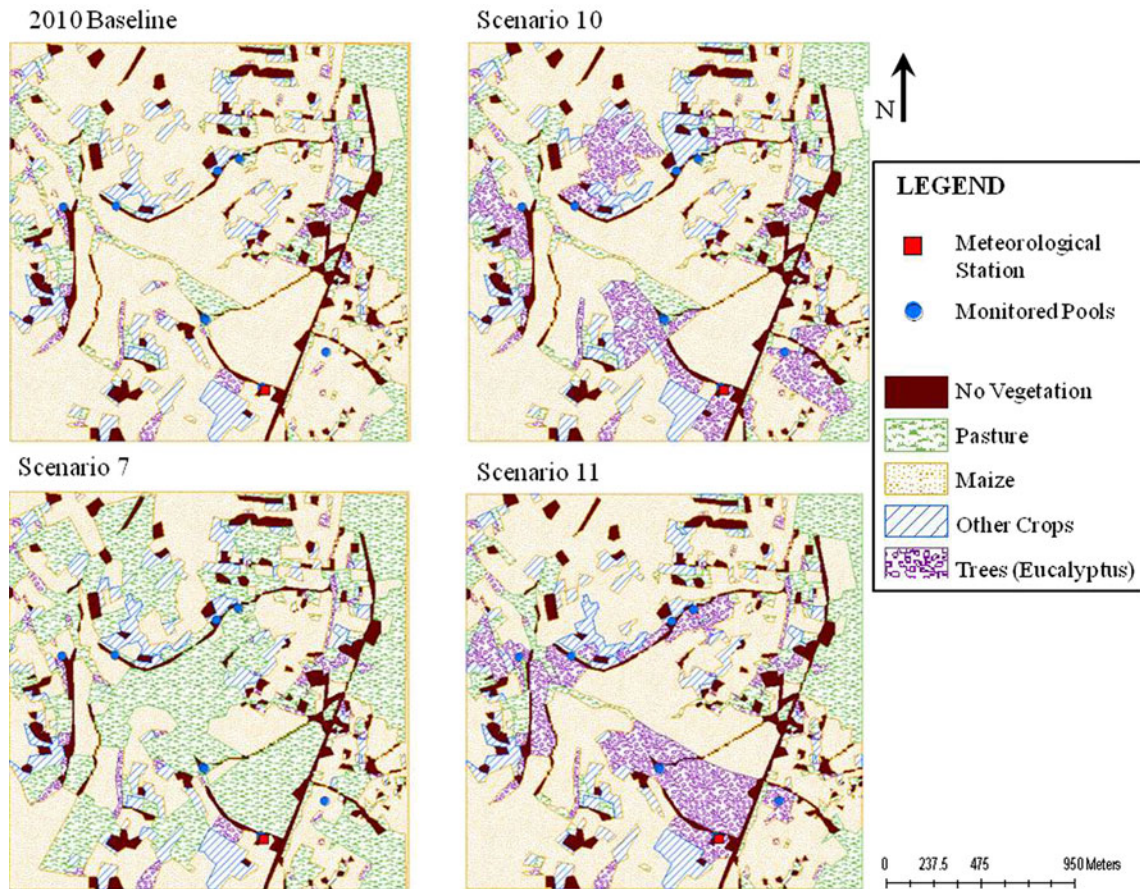


Fig. 10. GIS raster images of vegetation classification, including four of the scenarios listed in Table 3.

Increasing Manning's n and LAI resulted in lower mosquito abundance results, and the converse was true for decreasing those parameters. An increase in β produced higher mosquito abundance, and a decrease lowered abundance. Cumulative mosquito abundance results were most sensitive to changes in Manning's n .

DISCUSSION

The modeling approach used in this study quantifies the effects of land use change on hydrological processes leading to intraseasonal variation in mosquito abundance. The results of this study add to previous work linking land use with microclimate variables such as temperature and humidity, which in turn influence the development of the malaria vector and parasite, thereby shaping local mosquito population dynamics and malaria transmission (Lindblade et al. 2000; Patz and Olson 2006; Patz et al. 1998; Pascual et al. 2006). Warmer temperatures have been clearly associated with specific types of land use such as cultivated

swamps versus natural swamps (Lindblade et al. 2000), farmland habitats (Munga et al. 2006), and deforestation (Afrane et al. 2008; Yasuoko and Levins 2007; Minakawa et al. 2005; Olson et al. 2010). Variable amounts of shading, temperature, and evaporation are mechanisms by which land use affects the surface microclimates that can influence malaria transmission.

Results of this study indicate that not only land use type, but also spatial relations between land use and breeding habitats, may be an important influence on runoff reaching malaria vector breeding habitats in water-limited environments. The entomology model maintains the spatial structure of environmental variables, (such as pool locations, crop arrangement, and human positions), as well as of the mosquito population. Modifications made to vegetation parameters near breeding habitats had more effect than altering land further from these locations. This is expected, as most impounded water originates near the topographic low points, thus having moved over less of the infiltrating ground surface.

Preliminary insight gained here about the importance of spatial relations between breeding habitats and land

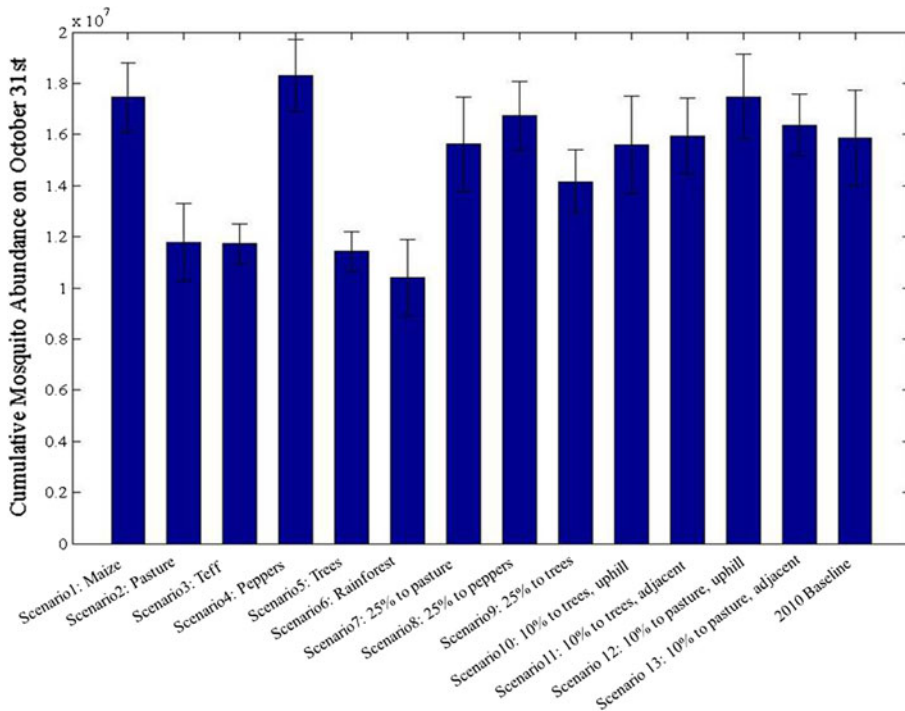


Fig. 11. Cumulative mosquito abundance at end of season (October 31st) for all scenario runs. Whiskers indicate 95th percentile confidence intervals based on 10 replicate runs.

cover types is supported by similar ideas presented in the field of landscape ecology and epidemiology. Landscape features affect the spatial heterogeneity in vectors, pathogens, and hosts, which is crucial to understanding transmission patterns of many diseases (Ostfeld et al. 2005; Kitron 1998; Reisen 2010). Tools such as GIS and remote sensing are being used to investigate and map components of disease transmission, including vegetation patterns. For instance, Bøgh et al. (2007) identified breeding mosquito habitats and mapped local scale variation in vector abundance and entomological inoculation rates (EIR) using landscape properties obtained from satellite imagery. Vegetation and landscape characteristics are critical environmental components that contribute to dynamic spatial variability in host, vector, and pathogen populations, by altering feeding patterns, habitat availability, dispersal and dispersion, and microclimates (Kitron 1998; Reisen 2010; Lindblade et al. 2000). Our study supports the idea that spatial layout and variability in land cover affects small-scale hydrological processes and thereby local vector population dynamics.

As with all modeling studies, several assumptions were made to minimize variability from unknown sources and focus modeling efforts on factors of interest. Mosquito abundance is limited by the presence of temporarily pooled water; this assumption was supported by field observations in this region of Ethiopia, as well as in other areas prone to

seasonal and epidemic malaria (Service 1993; Bomblies et al. 2008). Under environmental conditions in which water does not limit mosquito breeding, this mechanism may play a lesser role in influencing relative mosquito abundance.

Global climate change is expected to alter the distribution of areas suitable for malaria transmission (Peterson 2009; Lafferty 2009; Bomblies and Eltahir 2009), and expose new populations to the risk of infection. The 1958 and 1998 malaria epidemics in Ethiopia affected regions previously considered malaria free (Kiszewski and Teklehaimanot 2004; Abeku et al. 2003). In addition, climate-based models have predicted that increases in temperature and changes in rainfall patterns will result in a longer malaria season for many sub-Saharan African regions (Tanser et al. 2003; Lieshout et al. 2004). Land use change is also on the rise, including a huge expansion in the amount of land used for maize cultivation throughout much of sub-Saharan Africa (Houghton 1994). The replacement of natural ecosystems with agriculture brings about shallower root systems, lower evaporation rates, and higher runoff (Mumeka 2009; Calder et al. 1995), which improves conditions of *A. arabiensis* breeding habitats and results in a higher vectorial capacity. The effects of climate and land use change will also alter spatial relationships between hosts, vectors, parasites, and environmental conditions that interact to determine disease transmission characteristics

Table 4. Results of Runs to Assess Sensitivity of Mosquito Abundance Results to Vegetation Parameters, as Compared to the 2010 Baseline Scenarios Results

Vegetation parameter tested	Mosquito abundance results associated with 10% increase in parameter value (%)	Mosquito abundance results associated with 10% decrease in parameter value (%)
Manning's n	20.1% decrease	15.4% increase
LAI	18.2% decrease	2.3% increase
β	10.1% increase	0.6% decrease

(Kitron 1998). Understanding the mechanistic basis of relationships between environmental drivers and malaria will be increasingly valuable in a world affected by changing climate and land use conditions. Models capable of simulating the response to environmental conditions that fall outside of the range of previously observed variability will be dependent on these mechanisms.

CONCLUSIONS

Results of this study show a sensitivity of mosquito abundance to land use due to hydrological processes, and indicate a particular sensitivity to flow resistance associated with varying land cover types. This study neglected other potential land use/malaria linkages such as differences in radiation or the occurrence of microclimates, in order to isolate hydrological effects. We conclude that hydrological processes associated with land use change contribute to previously observed land use/malaria correlations attributed to microclimates. This is in addition to previously reported mechanisms, such as variations in near surface air temperature and nutrient availability in developmental habitat. Modeling results also indicate the importance of spatial relationships between land use and breeding habitats in simulating mosquito abundance dynamics. The ability of models to simulate small-scale hydrologic responses to land use changes, demonstrates their usefulness as a tool for understanding and predicting interannual and spatial variability in mosquito vector populations in response to exogenous changes from population growth, movement, and climate change.

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