

https://dspace.org/

Heterogeneous malaria transmission patterns in southeastern Tanzania driven by socioeconomic and environmental factors

Linda Mukabana; I Mshani; John Gachohi; E Minja; Fredos Okumu ...

https://hdl.handle.net/10539/48953
WOS

Downloaded from a DSpace repository. https://dspace.org/

Malaria Journal

RESEARCH

Open Access

Heterogeneous malaria transmission patterns in southeastern Tanzania driven by socio-economic and environmental factors

Linda N. Mukabana[1,2*], Issa H. Mshani[2,3], John Gachohi[1,4,5], Elihaika G. Minja[2,6], Frank M. Jackson[2], Najat F. Kahamba[2,3], Polius G. Pinda[2,8,10], Letus Muyaga[2], Dickson S. Msaky[2], Halfan S. Ngowo[2], Susan N. Mambo[1], Amos Olwendo[1], Donal Bisanzio[2,7] and Fredros O. Okumu[2,3,8,9]

Abstract

Background As malaria-endemic countries progress towards elimination, distinct patterns of heterogeneous transmission are emerging. In south-eastern Tanzania, despite intensive control efforts, localized transmission shows prevalence ranging from under 1% to over 50% among nearby villages. This study investigated the socioeconomic and environmental factors driving this spatial heterogeneity.

Methods A cross-sectional survey was conducted in the Kilombero and Ulanga districts of south-eastern Tanzania between 2022 and 2023, screening 3,249 individuals (ages 5–60) across 10 villages for malaria using rapid diagnostic tests (RDTs). Socioeconomic data was collected from all surveyed households and villages via questionnaires, while environmental data were obtained from remote sensing data sources. Associations between socioeconomic factors and malaria infection were analysed using a zero-inflated negative binomial model and employed a generalized additive model (GAM) to assess the impact of rainfall, and temperature on malaria infection.

Results Greater elevation and higher rainfall were positively associated with malaria infection (OR = 1.68, 95% CI 1.38–2.05, $p < 0.001$ and OR = 1.46, 95% CI 1.14–1.87, $p < 0.05$ respectively), while temperature showed no significant effect (OR = 0.70, 95% CI 0.51–1.13, $p = 0.117$). Households in densely vegetated areas had higher malaria infections compared to those in more developed, built-up areas. At the individual level, males had a higher prevalence (355; 28.6%) and displayed significantly greater odds of infection (OR = 1.53, 95% CI 1.15–2.03, $p < 0.05$) than females (433; 21.6%). School-aged children (5–17 years) had a higher prevalence (36.9%) compared to adults (18–60 years) (15.9%). The probability of infection declined with increasing age (OR = 0.28, 95% CI 0.25–0.31, $p < 0.001$). Larger household sizes (more than four members) were positively associated with malaria infection (OR = 1.72, 95% CI 1.29–2.29, $p < 0.001$). Open-eave housing was associated with higher odds of malaria, whereas closed eaves (OR = 0.56, 95% CI 0.38–0.82, $p < 0.05$) and metal roofs (OR = 0.62, 95% CI 0.44–0.87, $p < 0.05$) were protective factors. Open water sources were positively associated with malaria infection compared to protected water sources (OR = 0.57, 95% CI 0.38–0.85, $p < 0.05$). Lack of bed net use was positively associated with malaria but this was not statistically significant (OR = 1.54, 95% CI 0.68–3.48, $p = 0.299$).

*Correspondence:
Linda N. Mukabana
lindamukabana@gmail.com
Full list of author information is available at the end of the article

© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

Conclusion This study highlights the complex interplay between socioeconomic and environmental factors contributing to the fine-scale spatial heterogeneity of malaria in south-eastern Tanzania. Understanding these localized drivers is essential for designing targeted, effective strategies that support broader malaria elimination goals.

Background

Malaria is a major public health concern globally, accounting for 263 million cases and 597,000 fatalities worldwide in 2023 [1]. Tanzania was responsible for 3.3% of global malaria cases and 4.3% of the fatalities. Despite a significant decrease in the disease burden since 2000, challenges persist, including insecticide resistance, high costs of interventions, drug resistance and broader weaknesses in local economies and health systems [2].

The transmission of malaria, like many infectious diseases, often displays heterogeneous patterns, evident across spatial and temporal scales, as well as within host populations [3–5]. Effective control of the disease, therefore, requires a detailed understanding of these heterogenous patterns so that interventions can be more effectively targeted [6–8]. In most malaria-endemic regions, socioeconomic status [9] and environmental factors are critical determinants of malaria heterogeneity [10]

In a 2020 publication, the malaria stratification map of mainland Tanzania indicated that 40% of the population lived in very low to low prevalence zones, while 60% lived in areas identified as high prevalence strata [11]. The burden of malaria thus remains substantial, with an overall prevalence of 8% in mainland Tanzania [12] though the disease exhibits considerable geographical heterogeneity, with prevalence rates varying significantly across regions. Today, the central, northeastern and southwestern Tanzania regions report the lowest transmission intensities, while the southern, south-eastern and western regions experience a much higher burden [13].

In south-eastern Tanzania, an area once notorious for high malaria transmission, the widespread distribution of insecticide-treated nets (ITNs) and increased access to effective case management among other interventions have led to notable progress in reducing the disease burden. Although the region broadly continues to experience moderate to high malaria prevalence, certain areas within it have successfully achieved low transmission rates. Recent nation-wide surveys indicate varying prevalence rates in southeastern Tanzania, particularly in the regions of Pwani (7%), Morogoro (6%), and Mtwara (20%) [14].

As Tanzania progresses toward malaria elimination, understanding the heterogeneous spread of the disease at both regional and local levels within districts is critical [11, 15, 16]. This understanding will facilitate microstratification, allowing for targeted interventions including vector control measures; both indoors and outdoors, and housing modifications. In the vast Kilombero Valley, the prevalence of malaria remains inconsistent despite advancements to reduce malaria across the districts of Kilombero, Malinyi, and Ulanga [17]. Urban and peri-urban areas, such as Ifakara, report prevalence rates of less than 1%, while nearby villages can exceed 50% [17] This stark contrast in malaria transmission is perplexing, particularly in light of ongoing initiatives aimed at enhancing ITN distribution and improving access to effective case management.

Mapping these local-level variations in malaria transmission risk is crucial for developing targeted intervention strategies. Moreover, understanding the variations allows public health officials to identify transmission hotspots, enabling the allocation of resources to areas with the greatest need. Several approaches can be employed to achieve this, including geospatial analysis for visualizing and analysing spatial patterns of incidence [18, 19], ecological modelling to predict malaria transmission dynamics based on environmental and socioeconomic variables [19, 20], and community-based surveys that offer insights into local knowledge, behaviours, and practices influencing malaria risk [21, 22]. By integrating these methods, it is possible to develop comprehensive profiles of malaria transmission at finer scales, facilitating more effective and efficient control measures tailored to the unique circumstances of each community.

The aim of this study was to identify socioeconomic and environmental factors contributing to fine-scale spatial heterogeneity of malaria in south-eastern Tanzania, ultimately enhancing malaria control strategies, even in areas reporting low case numbers.

Methods

Study area

This study was conducted in the Morogoro region of southeastern Tanzania, specifically within the Kilombero and Ulanga districts, which lie between latitude − 7.6820 and − 9.9990 to the north and south, respectively and longitude 35.3150 and 37.8120 to the west and east, respectively. Ten villages were sampled, with five villages from each district (Kilombero: Sanje, Sululu, Kikwawila, Lungongole, Lipangalala; Ulanga: Kivukoni,

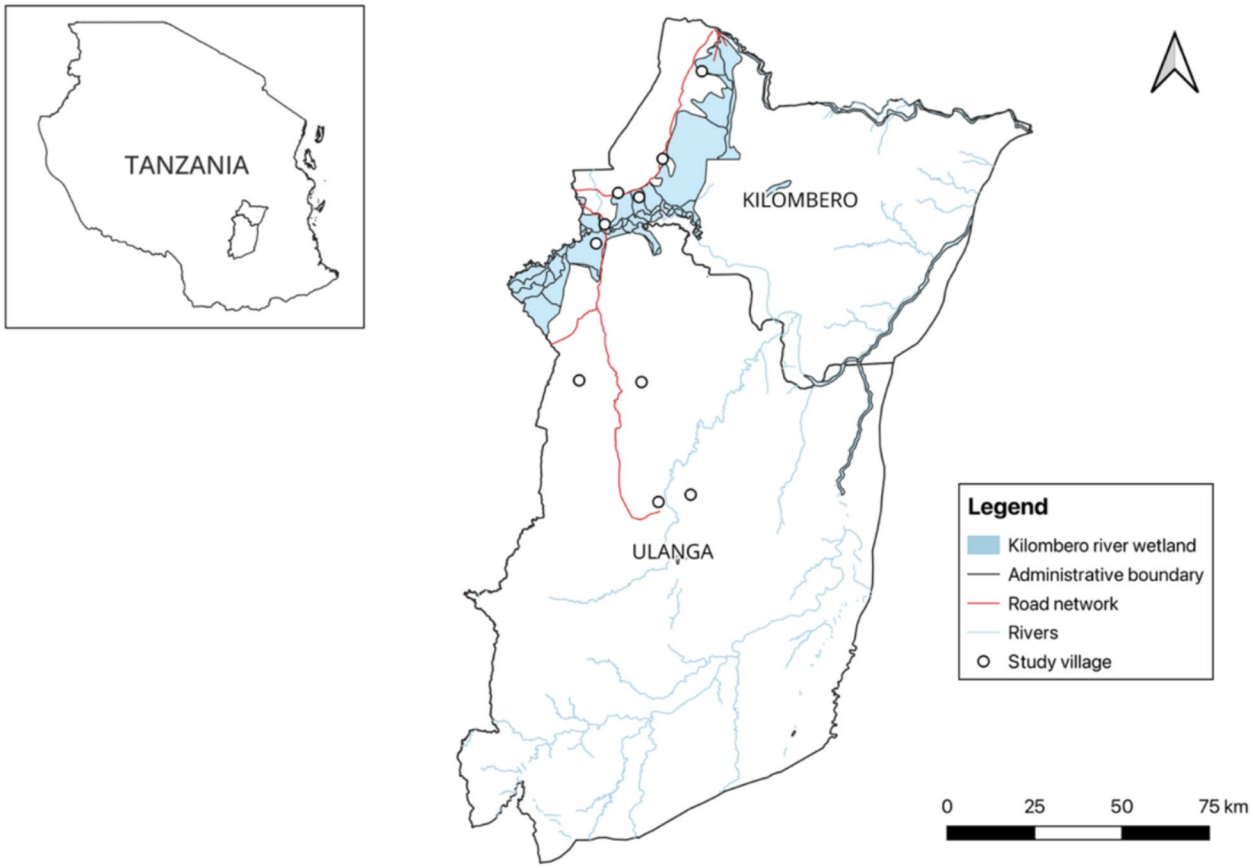


Fig. 1 Map of study area in south-eastern Tanzania; Kilombero and Ulanga districts

Chikuti, Msogezi, Mwaya, Mbuga) (Fig. 1). The area receives annual rainfall from 1200 mm in the low-lying plains and up to 2100 mm in the higher areas. About 90% of rainfall takes place during the wet season, which spans from December to April, while the dry season generally extends from June to September [23]. Annual mean temperatures range from 20 to 33 °C, and relative humidity varies from 70 to 80% [24]. The region's economy is primarily based on crop farming (including rice, maize and other crops), livestock keeping, and fishing.

Study procedures and survey tools

The malaria parasite prevalence data used for this analysis was obtained from a cross-sectional survey conducted once in each village from 2022 to 2023, during the months of April to September in both years [17]. Villages were purposively selected from each district to capture epidemiological variation in malaria prevalence, covering both low and high-altitude settings [17]. Sample sizes in each village were computed proportionally based on each village's population using the Cochran formula adjusted for finite populations [25–27]. For each village prevalence estimate, the sample size was designed to achieve a 95% confidence interval with a 5% precision [17].

Previous surveys and health centres in each village were used to determine the expected prevalence, which differed depending on the village. These unpublished surveys covered a significantly smaller proportion of the areas with prevalence ranging from 1 to 45%. Health facility data from the village or nearby villages were used for villages without these population surveys. Representative households were identified according to the estimated sample sizes for each village, presuming an average household size of four people. Households were selected using a randomization process based on the names of all household heads, provided by the respective village administrations. This ensured equal representation from each sub-village, facilitating thorough coverage of the entire village. The selected households were subsequently visited and recruited, upon providing consent. Additionally, the geo-location of each household was recorded using handheld GPS (Garmin GPSMAP 60 CSx; Garmin International Inc., Olathe, USA) to capture their coordinates.

The eligibility criteria involved individuals between the ages of 5 and 60 who had not received malaria treatment in the two weeks prior. This measure was taken to avoid potential overestimation by RDTs, which may identify residual traces following treatment [28]. Those requiring specialized medical care, such as pregnant women, were not included in the study. Eligible individuals from selected households were allowed to participate. Each household was assigned a unique identification number, prior to malaria screening. Every individual who consented to undergo malaria screening was also allocated a unique identification number that was linked to their respective household identification number. Blood samples were collected via finger prick on-site. RDT results were documented on a paper form, and individuals who tested positive for malaria were treated promptly using Artemether-Lumefantrine (ALu), following the established malaria treatment protocols of Tanzania [29].

Prior to the commencement of the survey, a five-day training program was held at the Ifakara Health Institute laboratory. This training comprised procedures for safeguarding human participants, study protocols, quality assurance, pilot implementations and training on data collection tools. The team included molecular laboratory technologists, licensed microscopists, clinical officers, and social scientists. The structured questionnaires used in this study were adapted from previous studies and other validated malaria surveillance tools, such as the Demographic and Health Survey (DHS) program instruments, including the Tanzania Malaria Indicator Survey. Enumerators, majorly social scientists, pre-tested the questionnaires in a few households and necessary adjustments were made to enhance the quality of the data collection tool. The questionnaires were developed in Kiswahili, spoken by an overwhelming majority of the residents, and administered to one adult respondent per household to avoid duplication of information. The survey collected socioeconomic data, including household size, toilet type, water source, bed net use, and house characteristics (roof, wall, and floor materials, window screens, and eaves). The full details of that epidemiological survey have been reported elsewhere by Mshani et al. [17].

This study focused on fine-scale stratification at the lowest administrative boundary; village level. The malaria risk categories used were; very low (< 1%), low (1–< 5%), moderate (5–< 30%), and high (≥ 30%). These *Plasmodium falciparum* parasite rate (*Pf*PR) categories were adapted from a study conducted in mainland Tanzania [11].

Geographical information

This study incorporated the following environmental factors: elevation, land cover, temperature, and rainfall. Elevation data was obtained using a high-resolution Digital Elevation Model (DEM) as described by Meyer et al. [30]. Land cover data of the study area were derived from satellite images sourced from the United States Geological Survey (USGS) Earth Explorer platform (http://earthexplorer.usgs.gov), with categories such as vegetation, crops, flooded vegetation, built-up areas, rangeland, water, and bare ground. Rainfall and temperature data were obtained at the village level using their respective shapefiles. Monthly temperature data was acquired in Kelvin (K) values from the Moderate Resolution Imaging Spectroradiometer (MODIS) datasets in Hierarchical Data Format (HDF), from January 2022 to December 2023. These data were converted to Tagged Image File Format (TIFF) format using Python version 3.10 and subsequently transformed to degrees Celsius (°C). Rainfall data was sourced from NASA's Precipitation Processing System (PPS) via the Integrated Multi-satellitE Retrievals for GPM (IMERG) Late Run dataset [31], available at a 10 km resolution (0.1°) for the period January 2022 to December 2023 in TIFF format. To extract point-level environmental data, these data were spatially linked to households using their respective coordinates; longitude and latitude.

Statistical analysis

Prior to analysis, the questionnaires were translated from Kiswahili to English. All RDT results were recorded in the Open Data Kit (ODK) system [32], and later exported as an Excel file for further cleaning. For individual-level risk factors, a generalized linear model (GLM) employing a binomial distribution was applied to assess the association between the risk of malaria infection and the predictors age and sex. This model treated individual malaria infection status (either positive or negative) as the binary outcome. To account for the clustering of individuals within villages, random effects for villages were included in this model.

Household-level factors associated with heterogeneous malaria were explored using a multivariable negative binomial regression model, with the counts of positive cases per household as the outcome variable, and all socioeconomic & environmental factors as predictor variables. To account for overdispersion, a zero-inflated negative binomial model was then fitted. The results were reported using odds ratios (OR) at 95% confidence intervals (CI) with $p < 0.05$ level of significance. For the variables temperature and rainfall, a generalized additive model (GAM) was fitted to test for their non-linear

effects on malaria infection. A cross-correlational analysis was performed on temperature by comparing mean monthly temperature and malaria infection, to determine the lag duration. Similarly, a cross-correlational analysis was also performed on rainfall comparing mean monthly rainfall and malaria infection. All analyses were performed using R statistical language V4.3.3, [33].

Ethical considerations

Ethical approvals for this study were obtained from the Ifakara Health Institute Review Board (Ref: IHI/IRB/No: 1/2021) and the National Institute for Medical Research (NIMR/HQ/R.8a/Vol. 1X/3735). Furthermore, approvals were secured from regional, district, ward, and the respective village authorities prior to starting the surveys, as the screening was conducted at a central location within each village. On the day before the test, each adult participant (as well as the parents or guardians of those under the age of 18) provided written informed consent.

Results

Characteristics of the study population

A total of 3249 individuals were sampled across 10 villages in Ulanga and Kilombero districts. In each village, about 132 to 449 individuals were tested for malaria using RDTs. Of these participants, 38.2% (1242) were male, and 61.8% (2007) were female (Table 1). School-going children (5–17 years) comprised 39.8% (1294) of

Table 1 Summary of study area characteristics and zero-inflated negative binomial model showing associations between these factors and malaria

Characteristic	Category	Total, n (%)	Malaria prevalence, n (%)	Odds ratio, OR [95% CI]	p-value
Sex	Female	2007 (61.8)	433 (21.6)	1 (reference)	
	Male	1242 (38.2)	355 (28.6)	1.53 [1.15–2.03]	< 0.05*
Age group (in years)	5–17	1294 (39.8)	477 (36.9)	1 (reference)	
	18–60	1955 (60.2)	311 (15.9)	0.28 [0.25–0.31]	< 0.001*
Household size	1–4	559 (51.4)	154 (27.5)	1 (reference)	
	5 +	529 (48.6)	189 (35.7)	1.72 [1.29–2.29]	< 0.001*
Eaves	Open	827 (76)	288 (34.8)	1 (reference)	
	Closed	261 (24)	55 (21.1)	0.56 [0.38–0.82]	< 0.05*
Window screens	Absent	704 (64.7)	258 (36.6)	1 (reference)	
	Present	384 (35.3)	85 (22.1)	0.89 [0.61–1.30]	0.541
Roof material	Thatch (Grass/banana leaves	367 (33.7)	167 (45.5)	1 (reference)	
	Metal (Zinc/iron/aluminum)	721 (66.3)	176 (24.4)	0.62 [0.44–0.87]	< 0.05*
Wall material	Earth/sand	300 (27.5)	120 (40)	1 (reference)	
	Plastered	113 (10.4)	12 (10.6)	0.82 [0.59–1.14]	0.248
	Bricks/cement	675 (62.1)	211 (31.3)	0.70 [0.29–1.69]	0.432
Floor material	Earth/sand	213 (19.6)	70 (32.9)	1 (reference)	
	Clay	528 (48.5)	211 (40)	0.96 [0.55–1.67]	0.874
	Tile	347 (31.9)	62 (17.9)	0.58 [0.17–1.98]	0.388
Toilet type	None	20 (1.8)	10 (50)	1 (reference)	
	Pit latrine	591 (54.3)	245 (41.5)	0.82 [0.40–1.70]	0.596
	Public improved	281 (25.8)	50 (17.8)	0.65 [0.27–1.57]	0.34
	Personal improved	196 (18.1)	38 (19.4)	0.58 [0.25–1.32]	0.193
Water source	Water body (spring, river, pond)	120 (11)	74 (61.7)	1 (reference)	
	Public open wells	93 (8.5)	43 (46.2)	0.77 [0.43–1.40]	0.396
	Public taps	720 (66.2)	189 (26.3)	0.75 [0.50–1.11]	0.144
	Protected/covered wells	155 (14.3)	37 (23.9)	0.57 [0.38–0.85]	< 0.05*
Bed net use	Yes	1041 (95.7)	320 (30.7)	1 (reference)	
	No	47 (4.3)	23 (48.9)	1.54 [0.68–3.48]	0.299
Elevation				1.68 [1.38–2.05]	< 0.001*
Rainfall				1.46 [1.14–1.87]	< 0.05*
Temperature				0.70 [0.51–1.13]	0.117

* indicates statistical significance

the population, while 60.2% (1955) were aged 18 years and above. The average household size was four, with higher malaria infections detected in households with more than four members, 35.7% (189), compared to 27.5% (154) in households with one to four members.

Physical characteristics of participant residences

In the complementary survey conducted to evaluate the characteristics of households that were tested for malaria, it was observed that the majority of houses (827; 76%) had open eaves, while a smaller portion had closed eaves (261; 24%). Most houses lacked window screens (704; 64.7%), with only 35.3% (384) having screened windows (Table 1).

Roofs were predominantly constructed from zinc, iron, or aluminum (721; 66.3%), with the remaining 33.7% (367) made from grass, thatch, or banana leaves. Regarding wall materials, 62.1% (675) of houses were built with bricks or cement, followed by those made of earth or sand (300; 27.5%) and plastered walls (113; 10.4%). Majority of the houses had floors made from clay (528; 48.5%) and tile (347; 31.9%), while fewer were made from earth/sand (213; 19.6%).

In terms of sanitation facilities, 54.3% (591) of households had pit latrines, 25.8% (281) had access to public improved toilets, 18.1% (196) had personal improved toilets, and 1.8% (20) had no toilet facilities (Table 1). The main sources of water were public taps (720; 66.2%), protected or covered wells (155; 14.3%), nearby water bodies (120; 11%), and public open wells (93; 8.5%).

Additionally, bed net use was significantly high, as a proportion of 95.7% (1041) households reported sleeping under a bed net the previous night.

Association of malaria parasite prevalence with demographic and socio-economic factors

Overall, malaria in the study area exhibited significant heterogeneity with prevalence ranging from 0% to about 60%. RDT-detected parasite prevalence in Ulanga district was found to be as high as 59.95% while Kilombero district reported prevalence as low as 0%. This substantial variation highlights the presence of micro-epidemiological differences in malaria transmission intensity. RDTs identified 2 villages as very low risk, 2 villages as low-risk, 3 as moderate risk and 3 in the high-risk strata.

*Pf*PR was higher among males and odds of infection were significantly greater compared to females (OR = 1.53, 95% CI 1.15–2.03) (Table 1). Age was a consistent risk factor for malaria infection in the study area. The probability of infection was almost three times higher among school-going children and declined as age increased into adulthood (OR = 0.28, 95% CI 0.25–0.31). It was also observed that larger household sizes were associated with increased malaria infection (OR = 1.72, 95% CI 1.29–2.29) (Table 1).

Housing structures exhibited a notable influence on malaria risk, further underscoring spatial variations in vulnerability. Households with closed eaves had significantly lower odds of malaria (OR = 0.56, 95% CI 0.38–0.82) compared to those with open eaves, a feature known to facilitate mosquito entry. Similarly, households with window screens had reduced malaria odds compared to those lacking screened windows (OR = 0.89, 95% CI 0.61–1.30), though this was not statistically significant (Table 1). Houses with metal roofs made of zinc, iron, or aluminum had lower odds of infection compared to those constructed from grass, thatch, or banana leaves (OR = 0.62, 95% CI 0.44–0.87). Natural materials such as earth, clay and sand that were used to construct the walls and floors of houses, were associated with higher odds of malaria infection compared to modern/advanced materials such as bricks or tile. However, these estimates were not statistically significant (Table 1).

Households with personal improved toilets had significantly lower risk of malaria infection (OR = 0.58, 95% CI 0.17–1.98) compared to those lacking sanitation facilities, with pit latrines or public improved toilets. Similarly, households that accessed water from protected or covered wells had lower odds of malaria compared to those relying on sources such as springs, rivers, ponds, public open wells, and public taps (OR = 0.57, 95% CI 0.38–0.85). To determine the utilization of preventive tools such as bed nets, bed net use the previous night was sought after as a proxy. Households that did not report the use of bed nets were about 1.5 times more likely to have malaria, but this was not statistically significant (OR = 1.54, 95% CI 0.68–3.48) (Table 1). Travel history was also collected during the survey to explore the role of human migration on malaria risk. However, data on household members'travel in the weeks preceding the survey was very limited, making it difficult to include this variable in the final statistical analysis. High-risk households were characterized by roofs, walls and floors made from natural materials, open eaves, poor sanitation facilities, using surface water as the main source and large household sizes.

Association between environmental factors and malaria parasite prevalence

The study area exhibited varying elevation, ranging between 150 and 600 m above sea level (Fig. 2). Elevation was positively associated with malaria infection according to the zero-inflated negative binomial model (Table 1). Contrary to numerous previous studies that suggest lower malaria prevalence at higher elevations, the findings indicated a significant positive association

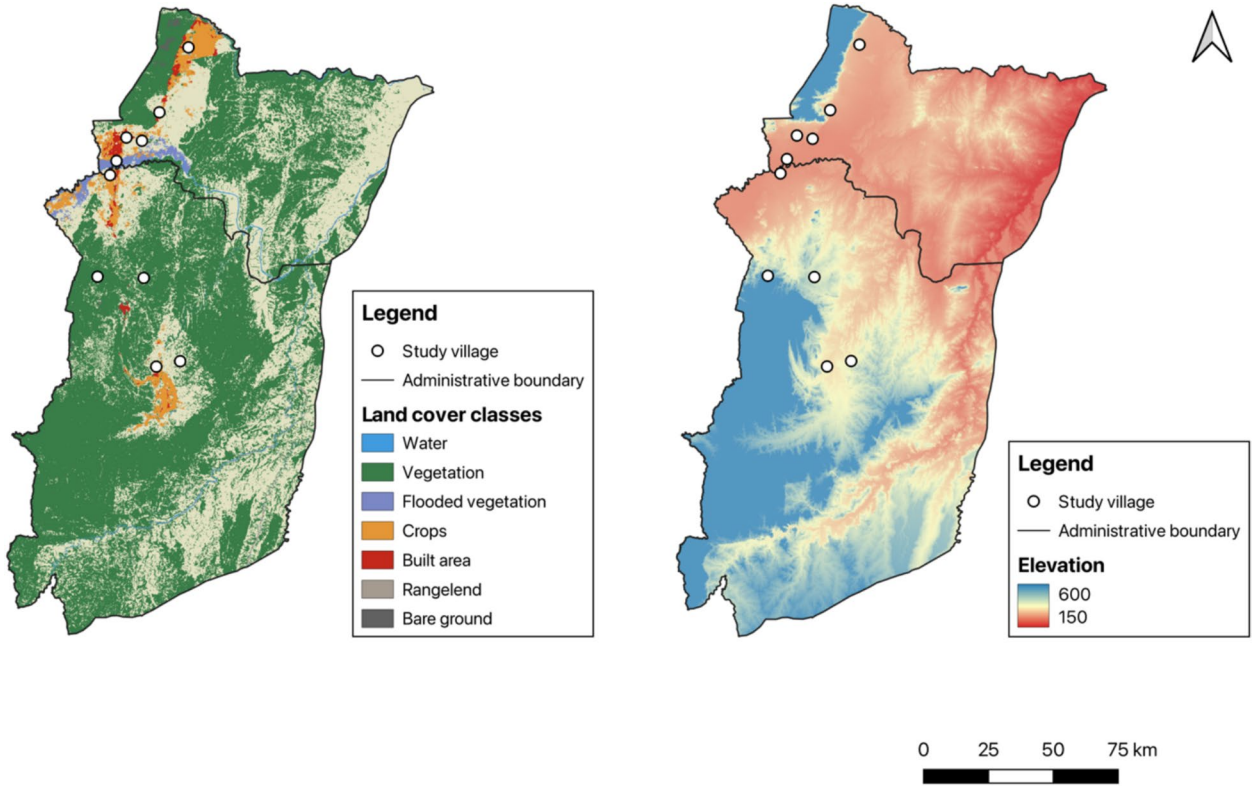


Fig. 2 Map of study area showing the distribution of elevation and land cover

Table 2 Distribution of land cover classes (in percentages) according to low, moderate and high malaria risk categories

Land Cover Class	Low (> 0–< 5%)	Moderate (5–< 30%)	High (≥ 30%)
Water	1.16	0.66	0
Vegetation	8.7	50.16	90.45
Flooded vegetation	8.73	0.25	0
Crops	49	2.21	0
Built area	8.94	0.16	0.08
Bare ground	0.08	0.7	0.44
Rangeland	23.36	45.85	9.03

between increasing elevation and malaria infection (OR = 1.68, 95% CI 1.38–2.05).

Land cover analysis was conducted to assess its spatial relationship with malaria risk. The distribution of land cover classes varied across malaria risk strata as shown in Table 2 and was a significant predictor of malaria infection [16]. Areas characterized by dense vegetation exhibited a markedly higher malaria infection compared to locations predominated by residential and commercial developments (Table 2). This finding aligns with the expectation that vegetation-rich environments provide suitable habitats for mosquito breeding and survival, thereby sustaining malaria transmission cycles.

Temperature within the study area ranged from 23.8 °C to 31.2 °C, with an average of 25.5 °C. Despite previous studies identifying temperature as a key factor influencing malaria transmission, the zero-inflated negative binomial model showed no statistically significant association between temperature and malaria infection in this study (OR = 0.70, 95% CI 0.51–1.13) (Table 1). However, further analysis using a Generalized Additive Model (GAM) revealed a strong non-linear relationship which implies that there was no direct relationship between temperature and malaria. The lack of a direct association may indicate the influence of other moderating factors, such as vector control interventions, housing characteristics, or human behaviour.

Rainfall varied significantly across the study area, ranging from 0 to 300 mm. It showed a positive association with malaria infection (OR = 1.46, 95% CI 1.14–1.87), with each additional millimeter of rainfall increasing the odds of infection (Table 1). The GAM analysis further confirmed this relationship, indicating that increased rainfall was linked to a rise in malaria cases, albeit with a slightly linear effect. This aligns with the well-established role of rainfall in creating suitable breeding conditions

for malaria vectors by increasing surface water availability for mosquito larval development.

To further investigate the temporal relationship between environmental factors and malaria occurrence reported in the survey, a cross-correlation analysis was conducted. The autocorrelation function (ACF) was used to examine the lag effect between environmental exposure and reported malaria cases. Temperature exhibited an immediate effect on malaria transmission, with no detectable lag, suggesting that short-term fluctuations in temperature may not substantially alter malaria risk in this setting. In contrast, rainfall demonstrated both an immediate effect and a delayed impact at one month, as shown in Fig. 3. The presence of a delayed effect suggests that while heavy rainfall may immediately enhance mosquito breeding conditions, its impact on malaria transmission becomes more pronounced after a short incubation period.

Spatially, high-risk households were concentrated in areas characterized by increased elevation, dense vegetation cover, and greater amounts of rainfall.

Discussion

Malaria exhibits spatial heterogeneity in tropical and subtropical regions like Africa [3–5]. Numerous studies identify socioeconomic status and environmental factors as key determinants of this heterogeneity [9, 10, 34]. This study revealed significant associations between malaria infection and both socioeconomic and environmental factors in southeastern Tanzania. Notably, higher elevation and increased rainfall were positively correlated with malaria infection. Housing characteristics, such as closed eaves and metal roofs, were identified as protective factors against malaria. Additionally, demographic factors like male gender, larger household sizes, and younger age groups were associated with higher malaria infection rates.

High elevation was associated with lower temperatures and higher rainfall. The positive correlation between elevation and malaria infection in this study area is intriguing, as it contrasts with the usual trend in other regions where higher elevations generally have lower malaria transmission due to cooler temperatures and fewer mosquito breeding sites [35, 36]. This anomaly likely arises because the altitudinal range investigated here was lower than in similar studies, with elevations under 1000 m still within suitable malaria transmission range [37]. In one study by Bodker et al. *i*n Tanzania's Usambara Mountains range, malaria transmission dropped 1000-fold from lowlands to highlands (300–1700 m) due to lower temperatures limiting vector density [38]. However, that study covered higher altitudes, with maximum elevations nearly triple those in this study area (600 m). This means that localized environmental conditions, such as rainfall, high vegetation, and suitable breeding sites for the main malaria vector, *Anopheles funestus*, likely drive this association, as this vector thrives in the high-ground habitats formed by river tributaries and specific vegetation types [19, 39]. Indeed, unlike *Anopheles gambiae*, *An. funestus* is known to thrive in areas with stable water bodies formed by these landscape features [19, 39, 40], suggesting that the local habitats play a critical role in supporting transmission even at the relatively higher altitudes.

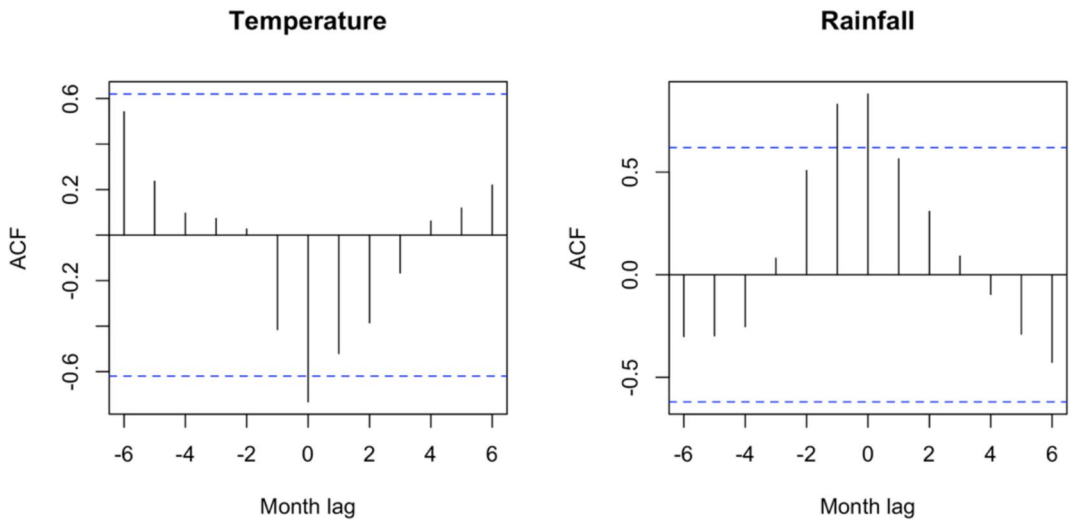


Fig. 3 Cross-correlation of both temperature and rainfall with malaria. The black vertical lines in each graph crossing the blue dotted threshold indicate significant correlation, $p < 0.05$

Furthermore, land cover characteristics, such as proximal water accumulation near households, significantly influence malaria infection, as shown in related studies [37, 39]. Socioeconomic factors unique to these elevated areas, such as differences in housing quality or limited access to preventive measures, may also contribute to this association. Thus, the interplay of environmental, topographical, and socioeconomic variables in this region creates conditions favorable to malaria transmission at high elevations, highlighting the need to consider local context when analysing altitude-related disease trends.

The strong correlation between rainfall and malaria infection reflects the role of increased rainfall in creating mosquito breeding sites, and possibly modulating humidity. Immediate and delayed impacts of rainfall suggest both direct effects on mosquito populations and indirect influences, such as increased standing water and human exposure during peak breeding periods. However, excessive rainfall may also temporarily disrupt transmission by washing away *Anopheles* larvae until habitats stabilize, allowing vector populations to recover [41]. Both seasonality and amount of precipitation have been positively associated with heterogeneous malaria patterns in this and other studies; for instance, in southeastern Tanzania, persistent rainfall correlates with higher malaria prevalence, while a study in Kenya showed that malaria nearly doubles with each additional mm of annual rainfall in regions with prolonged rainy seasons [42, 43]. The physical cover on the earth's surface also influences the presence of malaria vectors and, consequently, malaria infection [44]. This study found higher malaria infection in areas with dense vegetation and cropland compared to built-up or bare areas. It was also noted that densely vegetated regions are conducive to vector activity, contributing to heterogeneous malaria patterns across study sites [19, 45]. Malaria is positively associated with agricultural lands, such as rice and maize fields and pastured grasslands, and negatively associated with non-agricultural areas like bare land and shrubs [46]. In this study, this effect of land cover was particularly evident when comparing built-up areas with more pristine environments, as malaria transmission was significantly lower in built-up areas.

In addition to landscape-level environmental factors, this study also highlighted the significant role of physical house characteristics in influencing malaria infection at the household level. For example, houses with closed eaves and metal roofs were associated with a reduced risk of malaria, supporting previous findings that improved housing can effectively reduce mosquito entry and thereby lower transmission rates [47–49]. In this current study, it was observed that homes with thatched roofs or materials like grass were 1.6 times more likely to have malaria cases compared to those with metal roofs, likely due to the greater ease of mosquito entry. These results suggest that structural interventions, like improving roofing materials and closing eaves, could be valuable additions to existing malaria control strategies to enhance their effectiveness. However, contrasting evidence from Papua New Guinea suggests that roofs made of palm leaves or grass may reduce malaria odds, potentially due to increased openings for ventilation [45, 50]. This variation underscores the complexity of housing factors in different contexts but reinforces the broader role of housing in malaria prevention. However, when interpreted holistically, these findings advocate for incorporating housing improvements into malaria elimination programs, particularly in areas with high vector exposure.

Demographics also emerged as a critical factor influencing malaria infection in this study. Higher infection rates among males and school-aged children likely reflect behavioural patterns, such as spending time outdoors during peak mosquito activity or wearing less protective clothing. In this study area, men, in particular, may be exposed due to night-time outdoor activities like social gatherings, though such exposures may also occur in women in the peridomestic spaces [51, 52]. Some previous studies have similarly reported higher malaria prevalence among males, potentially due to increased outdoor exposure and skin exposure [43, 45]. In younger age groups, higher malaria prevalence may be related to outdoor activities like evening playtime, as noted in other studies [52–55]. It should be noted that this analysis did not include children under five due to their low representation in the epidemiological survey. Additionally, larger household sizes were positively associated with malaria risk in this study. Households with more members, an average size of four, had higher odds for malaria, likely due to greater collective exposure and increased mosquito attraction through human odours [56].

Across malaria-endemic countries, ITNs remain to be the most predominant control measure [1]. In this study, this is substantiated by the fact that up to 95.7% of the households utilize bed nets during the night, although not significantly associated with malaria infection. This is consistent with a number of studies indicating that the effectiveness of bed net use plateaued in further reducing human vector contact and malaria prevalence [45, 57, 58]. ITNs have also demonstrated no further effect in reducing malaria, following a rebound in malaria prevalence after a prolonged period of decline [59]. Consequently, this may indicate that vector biting was taking place before individuals were under a bed net or outdoors as documented in other settings [52, 60–62]. These findings highlight the importance of scaling up outdoor-focused interventions, such as topical repellents, spatial

repellents, and larval source management, to address risks for especially vulnerable groups [63].

Though broadly successful, this study also had some limitations that should be considered when interpreting the results. The cross-sectional design may have limited the ability to establish causality between the identified factors and malaria infection. Additionally, the reliance on RDTs for malaria diagnosis may have introduced diagnostic inaccuracies, potentially affecting prevalence estimates. Socioeconomic data were self-reported, which could be subject to reporting biases. Moreover, environmental data at a 10 km resolution might not capture micro-environmental variations that influence malaria transmission dynamics at a more granular level.

Conclusion

This study underscores how socioeconomic and environmental factors collectively shape fine-scale spatial heterogeneity of malaria transmission risk in southeastern Tanzania. Elevation, rainfall, housing characteristics, age, sex, and household size are key drivers of malaria within these villages. Understanding these localized factors is essential for implementing targeted control strategies that advance malaria elimination. Identifying high-risk areas allows for resource prioritization and interventions such as distributing insecticide-treated nets and conducting indoor residual spraying. Moreover, regular community education on proper usage of these prevention tools could enhance their protective effect.

Promoting housing modifications like closed eaves and metal roofs provides sustainable vector control, by reducing mosquito entry. Adoption of these improvements could be facilitated by community programs or government subsidies. Additionally, tailoring interventions for high-risk groups, including males and school-aged children, enhances prevention efforts. Integrating these intervention strategies can create synergistic effects, reducing malaria in high-risk areas. Future research should incorporate entomological studies to inform spatially targeted interventions, utilize longitudinal designs to establish causal links, and employ higher-resolution environmental data and qualitative studies on malaria-related behaviours to deepen understanding of local transmission and guide culturally appropriate strategies.

Abbreviations

ACF	Autocorrelation function
CI	Confidence interval
DEM	Digital elevation model
GAM	Generalized additive model
GLM	Generalized linear model
GPS	Global Positioning System
HDF	Hierarchical Data Format
IMERG	Integrated Multi-satellitE Retrievals for GPM
IRS	Indoor residual spraying
ITN	Insecticide-treated net
MODIS	Moderate resolution imaging spectroradiometer
MOH	Ministry of Health
NMCP	National Malaria Control Programme
ODK	Open Data Kit
OR	Odds ratio
*Pf*PR	*Plasmodium falciparum* Parasite rate
PMI	President's Malaria Initiative
PPS	Precipitation Processing System
QGIS	Quantum Geographic Information System
RDT	Rapid diagnostic test
TIFF	Tagged Image File Format
USGS	United States Geological Survey
WHO	World Health Organization

Acknowledgements

We extend our gratitude to Benson D. Makua, Jacob J. Nyooka, Festo I. Tangaliola and Tumpe G. Mwandyala for meticulous data entry. Additionally, the authors thank the staff at Ifakara Health Institute for their invaluable contribution, either directly or indirectly, to this study.

Author contributions

LNM, IHM, JG and FOO conceptualized and designed the study. LNM, IHM and FMJ were involved in data curation. LNM, IHM, PGP, DSM, LM, HSN, JG, DB and FOO analyzed the data. LNM, NFK and DSM produced the study site maps. LNM, DB and FOO contributed to the initial drafts of the manuscript. JG, AO, SNM, DB and FOO reviewed and revised the manuscript.

Funding

This work was supported in part by the Bill & Melinda Gates Foundation (Grant No. OPP 1217647 and Grant No. INV-002138 to Ifakara Health Institute). Under the grant conditions of the Foundation, a Creative Commons Attribution 4.0 Generic License has already been assigned to the Author Accepted Manuscript version that might arise from this submission. Support was also received from Rudolf Geigy Foundation through Swiss Tropical & Public Health Institute (to Ifakara Health Institute), Howard Hughes Medical Institute (HHMI) and Gates Foundation (Grants: OPP1099295) awarded to FOO and HMF, Royal Society (Grant No ICA/R1/191238 to SAB University of Glasgow and Ifakara Health Institute). Academy Medical Science Springboard Award (ref: SBF007\100094) to FB.

Availability of data and materials

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

This work was approved under Ifakara Health Institute Review Board (Ref: IHI/IRB/No: 1 2021) and the National Institute for Medical Research-NIMR (NIMR/HQ/R.8a/Vol. 1X/3735). Permission to publish this work has been granted by the National Institute for Medical Research-NIMR.

Competing interests

The authors declare no competing interests.

Author details

[1]School of Public Health, Jomo Kenyatta University of Agriculture and Technology, Nairobi, Kenya. [2]Environmental Health, and Ecological Sciences Department, Ifakara Health Institute, Morogoro, United Republic of Tanzania. [3]School of Biodiversity, One Health and Veterinary Medicine, The University of Glasgow, Glasgow, UK. [4]Global Health Programme, Washington State University, Nairobi, Kenya. [5]Paul G. Allen School of Global Health, Washington State University, Pullman, WA 99164, USA. [6]University of Basel, Petersplatz, 4001 Basel, Switzerland. [7]RTI International, Washington, DC, USA. [8]School of Public Health, The University of the Witwatersrand, Park Town, South Africa. [9]Nelson Mandela African Institution of Science and Technology, School of Life Sciences and Biotechnology, Arusha, United Republic of Tanzania. [10]Institute of Animal Sciences, Experimental Zoology Group, Wageningen University & Research, Wageningen, The Netherlands.

Received: 19 December 2024 Accepted: 16 May 2025
Published online: 29 May 2025

References

1. WHO. World malaria report 2024: addressing inequity in the global malaria response. 2024.
2. Cohen JM, Okumu F, Moonen B. The fight against malaria: diminishing gains and growing challenges. Sci Transl Med. 2022;14: eabn3256.
3. Woolhouse MEJ, Dye C, Etard J-F, Smith T, Charlwood JD, Garnett GP, et al. Heterogeneities in the transmission of infectious agents: implications for the design of control programs. Proc Ntl Acad Sci USA. 1997;94:338–42.
4. Bousema T, Baidjoe A. Heterogeneity in malaria transmission: underlying factors and implications for disease control. Ecology of parasite-vector interactions. Wageningen Academic; 2013. pp. 197–220.
5. Perkins TA, Scott TW, Le Menach A, Smith DL. Heterogeneity, mixing, and the spatial scales of mosquito-borne pathogen transmission. PLoS Comput Biol. 2013;9: e1003327.
6. Carter R, Mendis KN, Roberts D. Spatial targeting of interventions against malaria. Bull World Health Organ. 2000;78:1401–11.
7. Bisanzio D, Lalji S, Abbas FB, Ali MH, Hassan W, Mkali HR, et al. Spatiotemporal dynamics of malaria in Zanzibar, 2015–2020. BMJ Glob Health. 2023;8: e009566.
8. Kang SY, Battle KE, Gibson HS, Cooper LV, Maxwell K, Kamya M, et al. Heterogeneous exposure and hotspots for malaria vectors at three study sites in Uganda. Gates Open Res. 2018;2:32.
9. Yadav K, Dhiman S, Rabha B, Saikia PK, Veer V. Socio-economic determinants for malaria transmission risk in an endemic primary health centre in Assam. India Infect Dis Poverty. 2014;3:19.
10. Weiss DJ, Lucas TCD, Nguyen M, Nandi AK, Bisanzio D, Battle KE, et al. Mapping the global prevalence, incidence, and mortality of *Plasmodium falciparum,* 2000–17: a spatial and temporal modelling study. Lancet. 2019;394:322–31.
11. Thawer SG, Chacky F, Runge M, Reaves E, Mandike R, Lazaro S, et al. Sub-national stratification of malaria risk in mainland Tanzania: a simplified assembly of survey and routine data. Malar J. 2020;19:177.
12. Ministry of Health (MoH) [Tanzania Mainland], Ministry of Health (MoH) [Zanzibar], National Bureau of Statistics (NBS), Office of the Chief Government Statistician (OCGS), and ICF. Tanzania Demographic and Health Survey and Malaria Indicator Survey 2022 Final Report. Dodoma, Tanzania, and Rockville, USA. 2022.
13. Mandai SS, Francis F, Challe DP, Seth MD, Madebe RA, Petro DA, et al. High prevalence and risk of malaria among asymptomatic individuals from villages with high prevalence of artemisinin partial resistance in Kyerwa district of Kagera region, north-western Tanzania. Malar J. 2024;23:197.
14. U.S. President's Malaria Initiative Tanzania (Mainland). Malaria Profile. 2023.
15. Runge M, Thawer SG, Molteni F, Chacky F, Mkude S, Mandike R, et al. Sub-national tailoring of malaria interventions in Mainland Tanzania: simulation of the impact of strata-specific intervention combinations using modelling. Malar J. 2022;21:92.
16. Thawer SG, Golumbeanu M, Lazaro S, Chacky F, Munisi K, Aaron S, et al. Spatio-temporal modelling of routine health facility data for malaria risk micro-stratification in mainland Tanzania. Sci Rep. 2023;13:10600.
17. Mshani IH, Jackson FM, Minja EG, Abbasi S, Lilolime NS, Makala FE, et al. Comparison of fine-scale malaria strata derived from population survey data collected using RDTs, microscopy and qPCR in South-Eastern Tanzania. Malar J. 2024;23:376.
18. Okunlola OA, Oyeyemi OT. Spatio-temporal analysis of association between incidence of malaria and environmental predictors of malaria transmission in Nigeria. Sci Rep. 2019;9:17500.
19. Kahamba NF, Okumu FO, Jumanne M, Kifungo K, Odero JO, Baldini F, et al. Geospatial modelling of dry season habitats of the malaria vector, *Anopheles funestus,* in south-eastern Tanzania. Parasit Vectors. 2024;17:38.
20. Asori M, Musah A, Odei J, Morgan AK, Zurikanen I. Spatio-temporal assessment of hotspots and seasonally adjusted environmental risk factors of malaria prevalence. Applied Geogr. 2023;160: 103104.
21. Whittaker M, Smith C. Reimagining malaria: five reasons to strengthen community engagement in the lead up to malaria elimination. Malar J. 2015;14:410.
22. Finda MF, Kaindoa EW, Nyoni AP, Okumu FO. 'The mosquitoes are preparing to attack us': knowledge and perceptions of communities in south-eastern Tanzania regarding mosquito swarms. Malar J. 2019;18:56.
23. Ruth EP, Kashaigili JJ, Majule AE. Availability, access and use of weather and climate information by smallholder farmers in the Kilombero River Catchment, Tanzania. In: Singh BR, Safalaoh A, Amuri NA, Eik LO, Sitaula BK, Lal R, editors. Climate impacts on agricultural and natural resource sustainability in Africa. Berlin: Springer Nature; 2020. p. 489–506.
24. WorldData.info. Climate and important cities in East Coast in Tanzania incl. temperatures, humidity, rain days, sunshine, water temperature (Morogoro). https://www.worlddata.info/africa/tanzania/climate-east-coast.php. Accessed 13 May 2025.
25. Kasiulevičius V, Šapoka V, Filipavičiūtė R. Sample size calculation in epidemiological studies. Gerontologija. 2006;7:225–31.
26. Arya R, Antonisamy B, Kumar S. Sample size estimation in prevalence studies. Indian J Pediatr. 2012;79:1482–8.
27. Cochran WG. Sampling techniques. Hoboken: John Wiley & Sons; 1977.
28. Mouatcho JC, Goldring JPD. Malaria rapid diagnostic tests: challenges and prospects. J Med Microbiol. 2013;62:1491–505.
29. National Malaria Control Programme. National Guidelines for Diagnosis and Treatment of Malaria. Dar es Salaam United Republic of Tanzania; 2006.
30. Tachikawa T, Kaku M, Iwasaki A, Gesch DB, Oimoen MJ, Zhang Z, et al. ASTER global digital elevation model version 2-summary of validation results. USGS Report. 2011; p. 37.
31. Kelley O. The IMERG multi-satellite precipitation estimates reformatted as 2-byte GeoTIFF files for display in a Geographic Information System (GIS). 2020.
32. Hartung C, Lerer A, Anokwa Y, Tseng C, Brunette W, Borriello G. Open data kit: tools to build information services for developing regions. In: Proceedings of the 4th ACM/IEEE international conference on information and communication technologies and development. 2010. pp. 1–12.
33. Team RDC. R: A language and environment for statistical computing. 2010.
34. Heggenhougen HK, Hackethal V, Vivek P. The behavioural and social aspects of malaria and its control: an introduction and annotated bibliography. Geneva: World Health Organization; 2003.
35. Cohen JM, Ernst KC, Lindblade KA, Vulule JM, John CC, Wilson ML. Topography-derived wetness indices are associated with household-level malaria risk in two communities in the western Kenyan highlands. Malar J. 2008;7:40.
36. Mwakalinga VM, Sartorius BKD, Limwagu AJ, Mlacha YP, Msellemu DF, Chaki PP, et al. Topographic mapping of the interfaces between human and aquatic mosquito habitats to enable barrier targeting of interventions against malaria vectors. R Soc Open Sci. 2018;5: 161055.
37. Balls MJ, Bødker R, Thomas CJ, Kisinza W, Msangeni HA, Lindsay SW. Effect of topography on the risk of malaria infection in the Usambara Mountains, Tanzania. Trans R Soc Trop Med Hyg. 2004;98:400–8.
38. Bødker R, Akida J, Shayo D, Kisinza W, Msangeni HA, Pedersen EM, et al. Relationship between altitude and intensity of malaria transmission in the Usambara Mountains, Tanzania. J Med Entomol. 2003;40:706–17.
39. Nambunga IH, Ngowo HS, Mapua SA, Hape EE, Msugupakulya BJ, Msaky DS, et al. Aquatic habitats of the malaria vector *Anopheles funestus* in rural south-eastern Tanzania. Malar J. 2020;19:219.
40. Kaindoa EW, Ngowo HS, Limwagu AJ, Tchouakui M, Hape E, Abbasi S, et al. Swarms of the malaria vector *Anopheles funestus* in Tanzania. Malar J. 2019;18:29.
41. Paaijmans KP, Wandago MO, Githeko AK, Takken W. Unexpected high losses of *Anopheles gambiae* larvae due to rainfall. PLoS ONE. 2007;2: e1146.
42. Mwangungulu SP, Dorothea D, Ngereja ZR, Kaindoa EW. Geospatial based model for malaria risk prediction in Kilombero valley, South-eastern, Tanzania. PLoS ONE. 2023;18: e0293201.
43. Mategula D, Gichuki J. Understanding the fine-scale heterogeneity and spatial drivers of malaria transmission in Kenya using model-based geostatistical methods. PLoS Glob Public Health. 2023;3: e0002260.
44. Mutuku FM, Bayoh MN, Hightower AW, Vulule JM, Gimnig JE, Mueke JM, et al. A supervised land cover classification of a western Kenya lowland endemic for human malaria: associations of land cover with larval *Anopheles* habitats. Int J Health Geogr. 2009;8:19.

45. Gul D, Rodríguez-Rodríguez D, Nate E, Auwan A, Salib M, Lorry L, et al. Investigating differences in village-level heterogeneity of malaria infection and household risk factors in Papua New Guinea. Sci Rep. 2021;11:16540.
46. Zhong D, Wang X, Xu T, Zhou G, Wang Y, Lee M-C, et al. Effects of microclimate condition changes due to land use and land cover changes on the survivorship of malaria vectors in China–Myanmar border region. PLoS ONE. 2016;11: e0155301.
47. Lindsay SW, Emerson PM, Charlwood JD. Reducing malaria by mosquito-proofing houses. Trends Parasitol. 2002;18:510–4.
48. Tusting LS, Ippolito MM, Willey BA, Kleinschmidt I, Dorsey G, Gosling RD, et al. The evidence for improving housing to reduce malaria: a systematic review and meta-analysis. Malar J. 2015;14:209.
49. Kaindoa EW, Finda M, Kiplagat J, Mkandawile G, Nyoni A, Coetzee M, et al. Housing gaps, mosquitoes and public viewpoints: a mixed methods assessment of relationships between house characteristics, malaria vector biting risk and community perspectives in rural Tanzania. Malar J. 2018;17:298.
50. Jatta E, Jawara M, Bradley J, Jeffries D, Kandeh B, Knudsen JB, et al. How house design affects malaria mosquito density, temperature, and relative humidity: an experimental study in rural Gambia. Lancet Planet Health. 2018;2:e498–508.
51. Moshi IR, Manderson L, Ngowo HS, Mlacha YP, Okumu FO, Mnyone LL. Outdoor malaria transmission risks and social life: a qualitative study in South-Eastern Tanzania. Malar J. 2018;17:397.
52. Finda MF, Moshi IR, Monroe A, Limwagu AJ, Nyoni AP, Swai JK, et al. Linking human behaviours and malaria vector biting risk in south-eastern Tanzania. PLoS ONE. 2019;14: e0217414.
53. Baidjoe AY, Stevenson J, Knight P, Stone W, Stresman G, Osoti V, et al. Factors associated with high heterogeneity of malaria at fine spatial scale in the Western Kenyan highlands. Malar J. 2016;15:307.
54. Monroe A, Mihayo K, Okumu F, Finda M, Moore S, Koenker H, et al. Human behaviour and residual malaria transmission in Zanzibar: findings from in-depth interviews and direct observation of community events. Malar J. 2019;18:220.
55. Mukisa MC, Kassano JJ, Mwalugelo YA, Ntege C, Kahamba NF, Finda MF, et al. Analysis of the 24-h biting patterns and human exposures to malaria vectors in south-eastern Tanzania. Parasit Vectors. 2024;17:445.
56. Kaindoa EW, Mkandawile G, Ligamba G, Kelly-Hope LA, Okumu FO. Correlations between household occupancy and malaria vector biting risk in rural Tanzanian villages: implications for high-resolution spatial targeting of control interventions. Malar J. 2016;15:199.
57. Lwetoijera DW, Kiware SS, Mageni ZD, Dongus S, Harris C, Devine GJ, et al. A need for better housing to further reduce indoor malaria transmission in areas with high bed net coverage. Parasit Vectors. 2013;6:57.
58. Hetzel MW, Pulford J, Ura Y, Jamea-Maiasa S, Tandrapah A, Tarongka N, et al. Insecticide-treated nets and malaria prevalence, Papua New Guinea, 2008–2014. Bull World Health Organ. 2017;95:695.
59. Zhou G, Lee M-C, Githeko AK, Atieli HE, Yan G. Insecticide-treated net campaign and malaria transmission in western Kenya: 2003–2015. Front Public Health. 2016;4:153.
60. Russell TL, Govella NJ, Azizi S, Drakeley CJ, Kachur SP, Killeen GF. Increased proportions of outdoor feeding among residual malaria vector populations following increased use of insecticide-treated nets in rural Tanzania. Malar J. 2011;10:80.
61. Sougoufara S, Diédhiou SM, Doucouré S, Diagne N, Sembène PM, Harry M, et al. Biting by *Anopheles funestus* in broad daylight after use of long-lasting insecticidal nets: a new challenge to malaria elimination. Malar J. 2014;13:125.
62. Thomsen EK, Koimbu G, Pulford J, Jamea-Maiasa S, Ura Y, Keven JB, et al. Mosquito behavior change after distribution of bednets results in decreased protection against malaria exposure. J Infect Dis. 2017;215:790–7.
63. Killeen GF, Tatarsky A, Diabate A, Chaccour CJ, Marshall JM, Okumu FO, et al. Developing an expanded vector control toolbox for malaria elimination. BMJ Glob Health. 2017;2: e000211.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.