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Abstract

Large scale modes of climate variability, including the El Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD), have been shown to significantly impact mosquito-borne diseases in the Tropics, including malaria. However, the mechanistic cascade from ENSO and the IOD, to induced changes in regional climate and ultimately mosquito abundance and behaviour is poorly understood. Mosquito population dynamics, behaviour and their potential to transmit disease are all sensitive to micro-climatic conditions. The warm phase of ENSO (El Niño) tends to be associated with increased precipitation and outbreaks of various vector-borne diseases, while the cold phase (La Niña) can cause drought during the short rains over East Africa. The sensitivity of *Anopheles* mosquito population dynamics and host-seeking behaviour to ENSO and to the resulting micro-climatic conditions, were investigated in the Kilombero Valley in Tanzania. From June 2016 to September 2017, changes in the timing and intensity of the rainy seasons and temperature due to the ENSO 2016–17 were observed. Mosquitoes were collected using Centres for Disease Control and Prevention (CDC) light traps indoors and mosquito electrocuting traps in- and outdoors. Changes in abundance and biting behaviour of *Anopheles arabiensis* and *Anopheles funestus* were correlated with climate and micro-climate. The impacts of El Niño on climate and mosquito abundance were not clear. However, the study area experienced a drought due to La Niña during which both vector species declined significantly. *An. arabiensis* densities stayed more stable at higher temperatures and were found in higher numbers outdoors with respect to *An. funestus*. For both species, indoor temperature and season determined their host-seeking location, with higher temperatures and the wet season driving them outside. The study confirmed the influence of ENSO and micro-climate on malaria vector abundance and host-seeking behaviour, generating hypotheses for predicting the impact of future ENSO on malaria risk and vector control. Our observation of higher outdoor biting during warmer conditions indicates that indoor vector control strategies may become proportionally less effective during this time.

1. Introduction

Despite successful control efforts and a vast reduction in cases and deaths over the last decade, malaria is still

a major public health concern in many parts of the world (Bhatt *et al* 2015a, 2015b, WHO 2018). Over 90% of all malaria cases and deaths occur in sub-Saharan Africa, and malaria continues to be the most

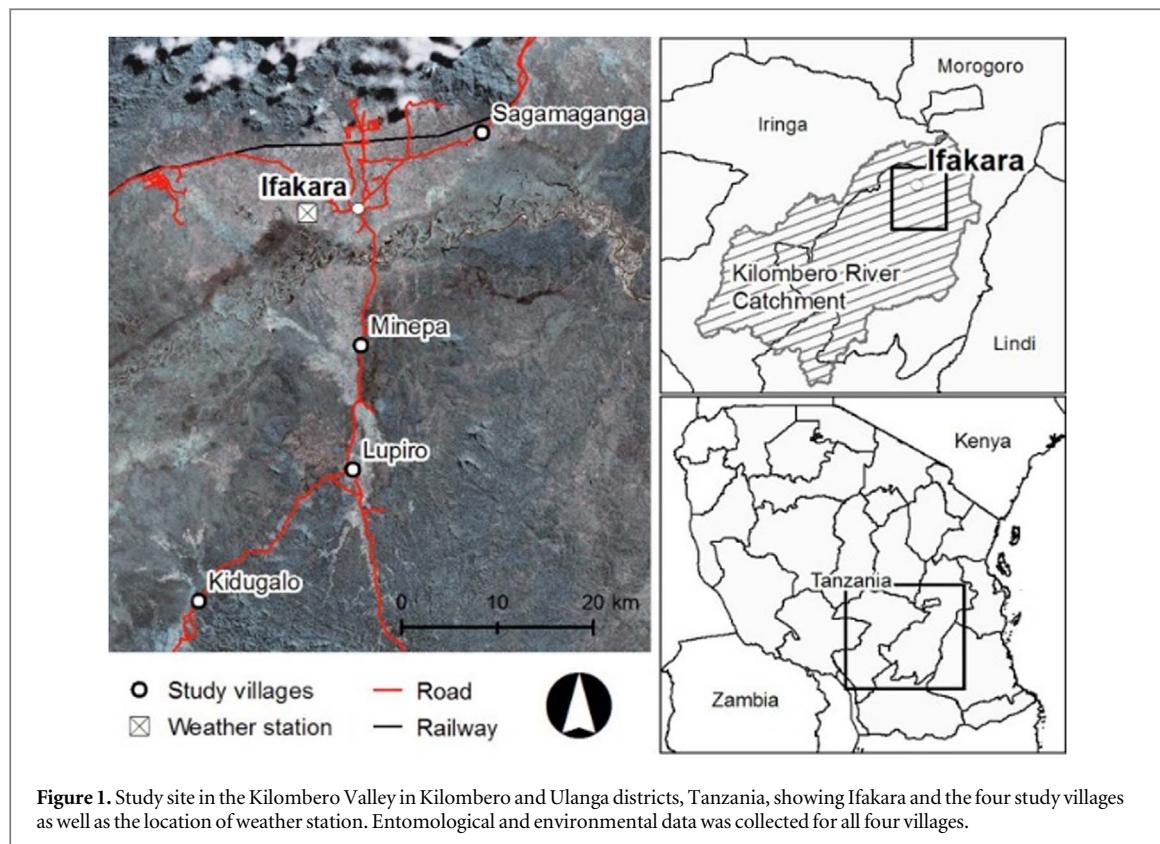
significant mosquito-borne disease hampering public health and socio-economic development in this region. The World Health Organisation estimated that there was an increase of two million cases between 2016 and 2017 globally (WHO 2018) and climate is considered a possible contributor. In most endemic regions of sub-Saharan Africa, mosquitoes of the *Anopheles gambiae* (*An. gambiae* s.s. and *An. arabiensis* its sibling species) and *Anopheles funestus* complex are the primary vectors for malaria (Collins and Besansky 1994, Donnelly *et al* 2001, Sinka *et al* 2012). There has been widespread and consistent demonstration of strong association between seasonal precipitation and abundance of these vectors because of the dependence of their aquatic larval stages on standing water (Lindblade *et al* 1999, Oesterholt *et al* 2006, Zhou *et al* 2007, Kelly-Hope *et al* 2009, Bomblies 2012). Additionally, other micro-climatic variables such as temperature have significant impacts on several aspects of adult vector fitness, behaviour and transmission potential (Bayoh and Lindsay 2003, Kulkarni *et al* 2006). For example, the gonotrophic cycle of mosquitoes (e.g. time between biting and laying eggs) shortens and adult survivorship increases with temperature up to a thermal tolerance threshold, beyond which their fitness is impaired (Paaijmans *et al* 2010). Additionally, the sporogonic development rate of malaria parasites within vectors increases with temperature, thus increasing their transmission potential (Shapiro *et al* 2017). These mosquito demographic and epidemiological parameters ultimately determine rates of human exposure to infected mosquito bites.

Micro-climatic and seasonal environmental variation can also impact human exposure to malaria in another way: by altering the timing and location where vectors bite. Currently, malaria vector control in Africa is primarily conducted through application of insecticides inside houses (Hemingway 2014). This is based on use of Long lasting Insecticidal Nets (LLINs) and Indoor Residual Spraying (IRS); both of which are very successful in reducing malaria in Africa (Bhatt *et al* 2015a, 2015b). The success of LLINs is based on their ability to exploit the behavioural predisposition of African malaria vectors to primarily feed on humans (anthropophagy) during sleeping hours, inside houses (endophagy), and rest indoors after feeding (endophily) (Lyimo and Ferguson 2009, Killeen *et al* 2017). These behaviours increase the probability of vectors coming into contact with insecticides either during host-seeking (e.g. LLINs) or resting on walls after blood feeding (e.g. IRS). Consequently, the upscaling of these control measures has coincided with a substantial decrease in malaria vector abundance (Bayoh *et al* 2010, The mal E. R. A. Consultative Group on Vector Control 2011), and the near eradication of highly anthropophagic and endophilic vectors, such as *An. gambiae*, in particular settings (Bayoh *et al* 2010, Russell *et al* 2010, Mwangangi *et al* 2013).

The host-seeking and resting behaviour of malaria vectors has previously been shown to be influenced by the micro-climate of their immediate environment (Paaijmans and Thomas 2011, Ngwo *et al* 2017). However, the relationship between larger-scale climate phenomena such as the El Niño Southern Oscillation (ENSO), micro-climate and mosquito host-seeking behaviour are less clear. Understanding the mechanistic cascade from the ENSO, to induced changes in regional climate, and ultimately mosquito abundance and host-seeking behaviour is important in times of a changing climate and increasing insecticide resistance. Indoor-based control methods may be increasingly challenged both by insecticide resistance and climate-driven changes in vector behaviour.

The Kilombero Valley in southern Tanzania has experienced historically high malaria transmission with 226 infective bites per person per year in 2012 (Lwetoijera *et al* 2014). Since then, it has seen a reduction in infective bites to 15.9 ib/p/yr in 2015 (Kaindoa *et al* 2017b, Finda *et al* 2018) due to control measures (LLINs and IRS). The availability of high quality historical data on vector ecology and transmission, and a high coverage with LLINs make this valley a good model for quantifying impacts of extreme climate events in areas of Africa where transmission has also been declining.

Worldwide the warm phase of ENSO, El Niño, is associated with the movement of warm waters from western part to the eastern part of the Pacific Ocean. El Niño has been associated with infectious disease outbreaks, including Rift Valley fever, malaria, and cholera; increased risk of arbovirus and malaria transmission in Latin America and Southeast Asia; and outbreaks of malaria and cholera in India (Hales *et al* 1999, Chretien *et al* 2015, Anyamba *et al* 2019). El Niño leads to a warming of the atmosphere in the Tropics which can last several months to a year after the event (Tyrrell *et al* 2015). El Niño often causes flooding over eastern Africa during the short rainy season (Oct to Dec), while its influence on the long rains (March–May) is less clear (Nicholson 2017). The effect of ENSO on malaria incidence in East Africa significantly varies regionally. During the 1958–59 El Niño, very conducive climate conditions resulted in three million additional malaria cases in the highlands of Ethiopia (Fontaine *et al* 1961). During the 1997–98 El Niño, higher temperatures and increased precipitation resulted in increased malaria prevalence in the highlands and north-eastern Kenya (Brown *et al* 1998). In contrast, an overall reduction of malaria cases was reported in the Usambara mountains of Tanzania during the 1997–98 El Niño which was attributed to heavy rainfall washing away mosquito breeding sites (Lindsay *et al* 2000). Conversely, an increase in malaria cases was reported at lower elevations for two other locations (Kagera and Morogoro) in Tanzania that year (Carlstedt *et al* 2004). The cold phase of ENSO, La Niña, tend to be associated with colder and drier conditions over East Africa (Omumbo *et al* 2011).



The relationship between La Niña, regional climate anomalies and malaria burden has not been extensively studied.

The Indian Ocean dipole (IOD) is an oscillation of sea surface temperatures (SSTs) in which the western part of the Indian Ocean becomes alternately warmer and then colder than the eastern part of the Indian Ocean. The positive phase of the IOD (when the western part is warmer than the eastern part of the Indian Ocean) has also been associated with flood conditions during the short rains (October–December) over Eastern Africa (Behera *et al* 2005). A positive phase of the IOD tends to increase easterlies crossing the Indian Ocean, bringing more moisture to eastern Africa during the short rains.

To fully understand the impacts of these climate anomalies on vector-borne diseases, thorough surveillance of vectors and their behaviour through all phases is needed. This study therefore aims to primarily determine the effects of ENSO 2016–17 on malaria vector abundance and host-seeking behaviour, as a means to understand the potential impact of these events on malaria transmission and to inform control strategies.

2. Methods

2.1. Study area

Mosquito vectors were collected in the Kilombero River Valley of southern Tanzania ($7^{\circ}44'$ to $9^{\circ}26'$ S/ $35^{\circ}33'$ to $36^{\circ}56'$ E) in four villages: Kidugalo, Lupiro,

Minepa and Sagamaganga (figure 1). The primary malaria vectors throughout this area are *Anopheles arabiensis*, (member of the *An. gambiae* s.l. complex) and *An. funestus* s.l. (Mwangangi *et al* 2013, Lwetoijera *et al* 2014, Mayagaya *et al* 2015, Finda *et al* 2018).

2.2. Experimental design

Entomological surveillance was carried out to investigate associations between climate variables and vector abundance, species composition and biting behaviour (biting time and location) between June 2016 and September 2017. Malaria vectors were repeatedly sampled in each village at the same four households for four consecutive days each month. On the first day of sampling, an index house was selected in each village on the basis of being accessible, and the presence and willingness of residents to participate. Three additional houses were recruited in the vicinity of the index house to achieve the required sample size (4 households), with houses being within 100–200 m of one another. In each set of houses, two houses were selected where livestock were kept (e.g. goats or cattle), and two without, because of the known impact on vector species composition and location of biting.

2.3. Trapping methodology

Two trapping methods were used to sample host-seeking mosquitoes throughout the study. CDC Miniature light traps were used to collect mosquitoes host seeking indoors at night. Additionally we introduced a relatively new sampling method; mosquito electrocuting traps (MET) which provide an exposure-free

method to directly measure mosquito landing rates on people in indoor and outdoor settings. METs can be used to sample mosquitoes attempting to feed on a human volunteer from 6 pm to 6 am in indoor and outdoor settings (Maliti *et al* 2015, Govella *et al* 2016). In June 2016 host-seeking mosquitoes were collected with CDC light traps in four houses for four nights in each village. From July 2016, CDC light traps were used in three out of the four houses, with METs being used at the remaining house (one indoors and one outdoors). Trap types were rotated each night following a Latin square design. These methods were selected because Centers of Disease Control and Prevention (CDC) light traps provide a widely used proxy of overall mosquito abundance and indoor biting rates (Briët *et al* 2015), while MET traps give information on hourly biting time and location. CDC light traps were deployed from 6 pm to 6 am every night by placing them approximately 1.5 m above ground and close to the foot of a bed in which between one and four people were sleeping under a LLIN. Collections with METs were also conducted from 6 pm to 6 am. The MET is composed of four electrified panels positioned in a square surrounding the lower legs of a seated volunteer, that intercept and kill mosquitoes on approach, while the rest of the volunteer's body is protected by netting. Each hour, the MET was turned off for 15 min to allow mosquitoes caught on the surface to be removed, recorded and stored. At the house allocated for MET collection, one trap was positioned within a living room and another outside (~5 m from house), on each night as described elsewhere (Govella *et al* 2016). The volunteers sitting in the MET traps were swapped between indoor and outdoor trapping stations every hour to minimise bias due to differing attractiveness to mosquitoes. Additional data on mosquito abundance and species composition based on CDC light trap collections (indoors) from a previous study (2012–2015, Kreppel *et al* in preparation) in the same villages (350 households) were used as a baseline for comparison with non-El Niño years.

2.4. Mosquito identification and molecular analyses

All mosquitoes collected in traps were killed by chloroform. The number and sex of those morphologically identified as belonging to the *An. gambiae* s.l or *An. funestus* s.l. complex or *Culex* species were recorded (Edwards 1941, Gillies and De Meillon 1968, Gillies and Coetzee 1987). A subset of *An. gambiae* s.l. collected ($n = 5600$, 22% of total) were identified to species level by polymerase chain reaction (PCR) (Scott *et al* 1993). For this, 5 individual mosquitoes were sampled from each trap per night. Mosquitoes were sampled for indoor and outdoor MET separately. With an amplification rate of 92.5%, laboratory results confirmed them all to be *An. arabiensis*. On this basis of the predominance of *An. arabiensis* in the *An.*

gambiae s.l. tested here and in other concurrent studies in the area (Govella *et al* 2009, Marsden *et al* 2014, Maliti *et al* 2015, Kaindoa *et al* 2017a), all *An. gambiae* s.l. collected were assumed to be, *An. arabiensis*. PCR analysis was also conducted on members of the *Anopheles funestus* s.l. to identify them to species level ($n = 2104$, 20% of total, amplification rate 87.6%) (Koekemoer *et al* 2002). The majority of *An. funestus* s.l. specimens were identified to be *An. funestus funestus* (97%) followed by *An. rivulorum* (1.4%) and *An. funestus lessonii* (1.1%). Additionally, mosquitoes were pooled in batches of a maximum of 10 per sampling tube per trap type, per night (*An. arabiensis*: $n = 14\,700$, 59% of total and *An. funestus*: $n = 7890$, 75% of total) Enzyme Linked Immunosorbent Assays were used to test for presence of *Plasmodium* malaria parasites (Beier *et al* 1990).

2.5. Environmental data

Indoor temperature and humidity were recorded with Tiny Tag Plus 2 data loggers (Gemini data loggers, UK, Ltd) placed inside houses on each night of sampling (approximately 1 m above the ground). These data were used to calculate the indoor saturation deficit for each house using established methods (Allen *et al* 1998). Season was defined for each sampling month as wet or dry depending on the monthly amount of rainfall. A month with rainfall over 1 mm per day on average was defined as 'wet'.

Daily climate data was retrieved from different sources. Daily rainfall (mm) and temperature (°C) were obtained from the Ifakara GloBe weather station (GRWS 100 Campbell Scientific) installed at the Ifakara Health Institute (IHI) (8.114 17 °S, 36.674 84 °E) within the floodplain (see figure 1). The weather station has been recording from 18th November 2014. To calculate anomalies (e.g. departure from the long term means), we utilised gridded climate data. Daily rainfall data from the Climate Hazards group Infrared Precipitation with Stations (CHIRPS) dataset at $0.05^\circ \times 0.05^\circ$ spatial resolution was used for the period 1981–2017 (Funk *et al* 2015). Monthly gridded temperature data ($0.5^\circ \times 0.5^\circ$ resolution) which combines weather station data from the Global Historical Climatology Network version 2 with the Climate Anomaly Monitoring System was utilised for the same period (Fan and van den Dool 2008). Monthly anomalies were calculated with respect to the 1981–2017 period for the gridded products. A comparison between gridded and weather station data is provided for rainfall on figure S1 is available online at stacks.iop.org/ERL/14/075009/mmedia and for temperature on figure S2. Time variability is well reproduced by the gridded data; but both CAMS and CHIRPS data tend to overestimate temperature and rainfall over Ifakara. The Nino 3.4 index data (calculated as monthly sea surface temperature anomalies with respect to 1981–2010 climatology over the region 5°N – 5°S and

Table 1. Number of mosquitoes collected throughout the study by species, sex and abdominal status in Centre for Disease Control and Prevention light traps and mosquito electrocuting traps.

Species	CDC light trap					
	Male	Unfed	Gravid	Fed	Total female	Total
<i>An. arabiensis</i>	1025	17836	152	805	18793	19818
<i>An. funestus</i>	1006	6925	395	440	7760	8766
Culex	1	NA	NA	NA	114	115
Other <i>Anopheles</i>	NA	NA	NA	NA	NA	100
Mosquito electrocuting trap						
<i>An. arabiensis</i>	113	5501	47	374	5922	6035
<i>An. funestus</i>	40	2415	90	239	2744	2784
Culex	7	NA	NA	NA	97	104
Other <i>Anopheles</i>	NA	NA	NA	NA	NA	138

170–120°W) and the Dipole Mode Index (calculated as the difference between the average SST in the region 50–70°E and 10°S–10°N minus the average SST in the box 90–110°E and 10°S–0°N) based on the HadISST data (Rayner *et al* 2003) were downloaded from KNMI climate explorer (Trouet and van Oldenborgh 2013).

2.6. Ethics

Before the study began, meetings were held with community leaders in all villages during which they were informed about the purpose of the study and their participation requested. After their permission had been granted, the study team visited each village and informed consent was obtained from each head of household where mosquito trapping was conducted. The study was previously approved by the Ifakara Health Institutional Review Board (Institutional Ethics Clearance: Certificate number IHI/IRB/No: 037-2016). It was further approved by the University of Liverpool ethics board (RETH001036).

2.7. Analysis and models

The potential environmental drivers of vector abundance and host-seeking location (indoors versus outdoors) were investigated in generalised linear mixed models (GLMMs) that included explanatory variables of nightly minimum, mean and maximum temperature (in °C) and relative humidity (RH in%) indoors, saturation deficit indoors (in kPa) and season (wet or dry). Effects of temperature, humidity and saturation deficit on mosquito abundance and host-seeking location were investigated using generalised linear mixed models with the ‘glmmTMB’ package in R statistical software (Brooks *et al* 2017). Mosquito abundance was estimated as the mean number of vectors caught per CDC light trap per night and in MET per hour. In all models, all micro-climatic variables and season were fitted as fixed effects while household id, date and trap number were fitted as random effects. Model selection was conducted using the Akaike Information Criterion (AIC), by

sequentially selecting models with lower AIC values and the rule of parsimony (Bolker *et al* 2009). For the models on host-seeking location, the hourly number of mosquitoes collected by MET was fitted as the response variable, while trap location (in- or outdoors) was fitted as a two-way interaction term to all fixed effects. Hour of collection was included as random effect nested in house. Data was modelled as following a negative binomial distribution due to the degree of overdispersion in the data (using a test for overdispersion by Cameron and Trivedi 1990).

3. Results

3.1. Mosquito bionomics

A total of 28 799 mosquitoes were collected using CDC light traps during 778 trap nights across the study (table 1). A further 9061 mosquitoes were collected with METs (combined indoors and outdoors), across 215 trap nights. With both methods, more than twice as many *An. arabiensis* were caught than *An. funestus*, with the majority of collected female mosquitoes unfed (table 1). Infection rates with *Plasmodium falciparum* were 0.013% for *An. arabiensis* and 0.025% in the *An. funestus*.

3.2. ENSO, regional climate anomalies and mosquito dynamics

The 2015–16 El Niño was one of the strongest events on record. This event started in October–November 2014, peaked during the boreal winter 2015 before declining during the boreal spring 2016. This warm event was followed by a mild La Niña signal from June 2016 to January 2017 (figures 2(a) and S3(a)). The SST signal in the Indian Ocean was not very clear in 2016; however, a moderate positive phase of the IOD occurred in 2017 (figure 2(a)). In Ifakara, rainfall tends to occur from November until May, with a peak in March–April (figures 2(b) and S3(c)). During the study period from June 2016 to September 2017, mean monthly temperature oscillated between 23 °C

and 30 °C (figures 2(b) and S3(b)). The warmest months are usually between October and January (figure S3(b)).

On average, the positive (negative) phase of ENSO, El Niño (La Niña), is associated with increased (decreased) rainfall conditions over eastern Africa during the short rains (figure S4(g)). The positive (negative) phase of the IOD is also associated with increased (decreased) precipitation over Tanzania (figure S4(h)). The relationship between rainfall in Tanzania and the IOD is even more pronounced than ENSO during the short rains as shown by Behera *et al* (2005). One of the wettest short rain season occurred in 1997 in Tanzania, when both positive phases of the IOD and ENSO co-occurred (figure S4(b)). In 2015, wetter than average conditions were observed over Tanzania (figure S4(c)), however, 2015 was not as wet as 1997. La Niña events in 1982, 1997 and 2016 were mostly related to drier than average conditions in Tanzania (figures S4(d)–(f)). The relationship between ENSO, DMI and land temperature in Tanzania is not significant and not clear, when long term trends are removed (figure S5). However, colder than average conditions are associated with the positive phase of the DMI (figure S5(h)) over northern Tanzania. This temperature signal is consistent with increased rainfall conditions (figure S4(h)) which tend to cool the land surface.

Anopheles arabiensis density peaked in phase during the February–April rainy reason, with *An. funestus* peaking 2–3 months later (May–August with a peak in July, see figures 2(c) and S3(d)). Despite some differences across study sites, this feature was relatively robust around the Kilombero Valley (figure S6). Climate anomalies (e.g. departures from the long term mean), warmer (colder) temperatures were experienced during El Niño (La Niña) events in Ifakara (figure S7(b)). During El Niño 2015–16, more rainfall was observed over the region (figure S7(c)). Conversely, a significant drought occurred during the following La Niña between October 2016 and February 2017 (figure S7(c)). These results for Ifakara are consistent with the aforementioned findings at country scale (figures S4 and S5).

Populations of both *Anopheles* vector species crashed below detection during the drought associated with La Niña (October 2016–February 2017). Drought conditions (figure S7(c)) and lower abundance (figure S7(d)) were previously observed from January to March 2012. The relative population crash was more pronounced for *An. funestus* than *An. arabiensis* (figure S7(d)). Lagged monthly correlations between temperature and mosquito abundance were not significant using a standard Pearson test except when temperature was leading *An. arabiensis* abundance by 1, 4 and 5 months (figures S8(a) and S8(b)). However, rainfall was significantly positively correlated with *An. funestus* at a 2 months lag ($r = 0.64$, $p < 0.001$, figure S4(d)).

3.3. Effects of micro-climate on host seeking location and abundance

More *An. arabiensis* were caught outdoors than indoors (figures 3(a), (c) and S9) while the opposite was observed for *An. funestus* (figures 3(b), (d) and S9(b)). No mosquitoes were caught when night-time relative humidity dropped below 40% (figure 3), with vector abundance highest when RH > 60%. Very few *An. funestus* were caught when mean temperature exceeded 32 °C (figures 3(b) and (d)). In contrast, the abundance of *An. arabiensis* was relatively stable between 24 °C and 32 °C, and the maximum suitable temperature was found to be 32 °C (figure 3(a)).

The mean number of *An. arabiensis* collected per CDC trap per night was negatively associated with maximum indoor temperature and showed a positive association with the wet season (table 2(a)). The abundance of *An. funestus* catches was negatively associated with increasing temperature (minimum and maximum, table 2(b)).

Exophily, defined as the relative proportion of mosquitoes caught in outdoor versus indoors METs, was predicted to increase in the wet season for both vector species outdoors of the total MET catch (table 2(c)).

An. arabiensis and *An. funestus* exhibited differences in the timing of their nightly host seeking (figure 4). Specifically, *An. arabiensis*, was very active from early evening (18.00) until midnight, mostly outdoors (figure 4(a)). Biting rates of *An. arabiensis* decreased after midnight following the observed decrease in temperature (figure 4(c)) and increase in RH (figure 4(d)). A secondary peak in *An. arabiensis* biting activity was observed in the early morning hours, when temperature increases again (06.00). Conversely, *An. funestus*, which was mostly caught indoors, was most active in the middle of the night between 23.00 and 01.00 (figure 4(b)).

4. Discussion

In the face of climate change impacts on East Africa, understanding the effects of climate (synoptic scale) and micro-climate on disease vector abundance and behaviour is essential. We investigated the relationship between ENSO, regional climate and micro-climate on two major malaria vector populations, *An. arabiensis* and *An. funestus*, in Tanzania.

Because of the juxtaposition of ENSO onto global warming in 2016–17, the Kilombero Valley in Tanzania, an area of historically high malaria transmission, has seen changes in the timing and intensity of the rainy seasons and temperature. In turn, the effect of ENSO on the malaria vector populations in the Kilombero Valley proved to be complex and vector specific.

The relationship between the 2015–16 El Niño, regional climate anomalies and the *Anopheles*

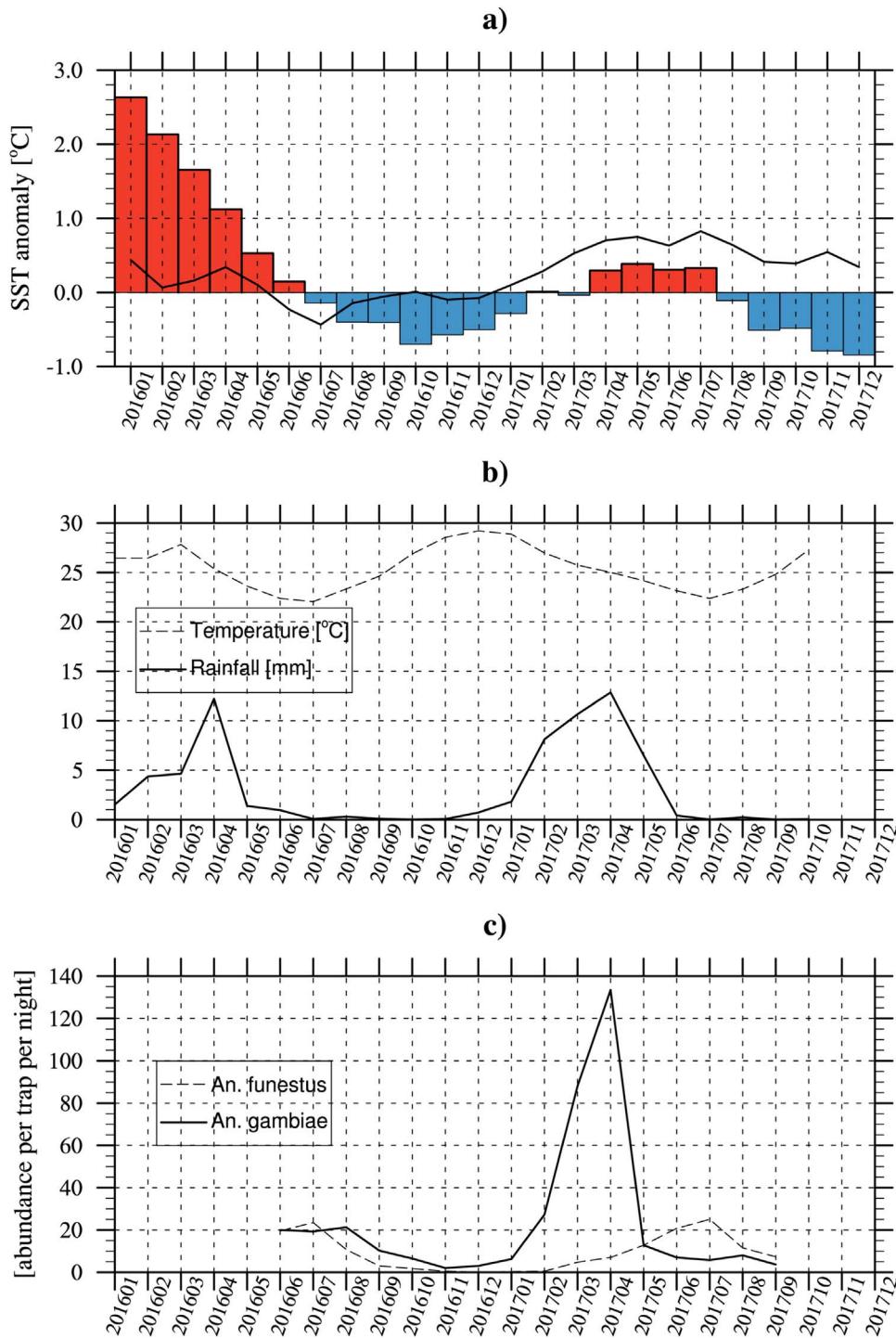
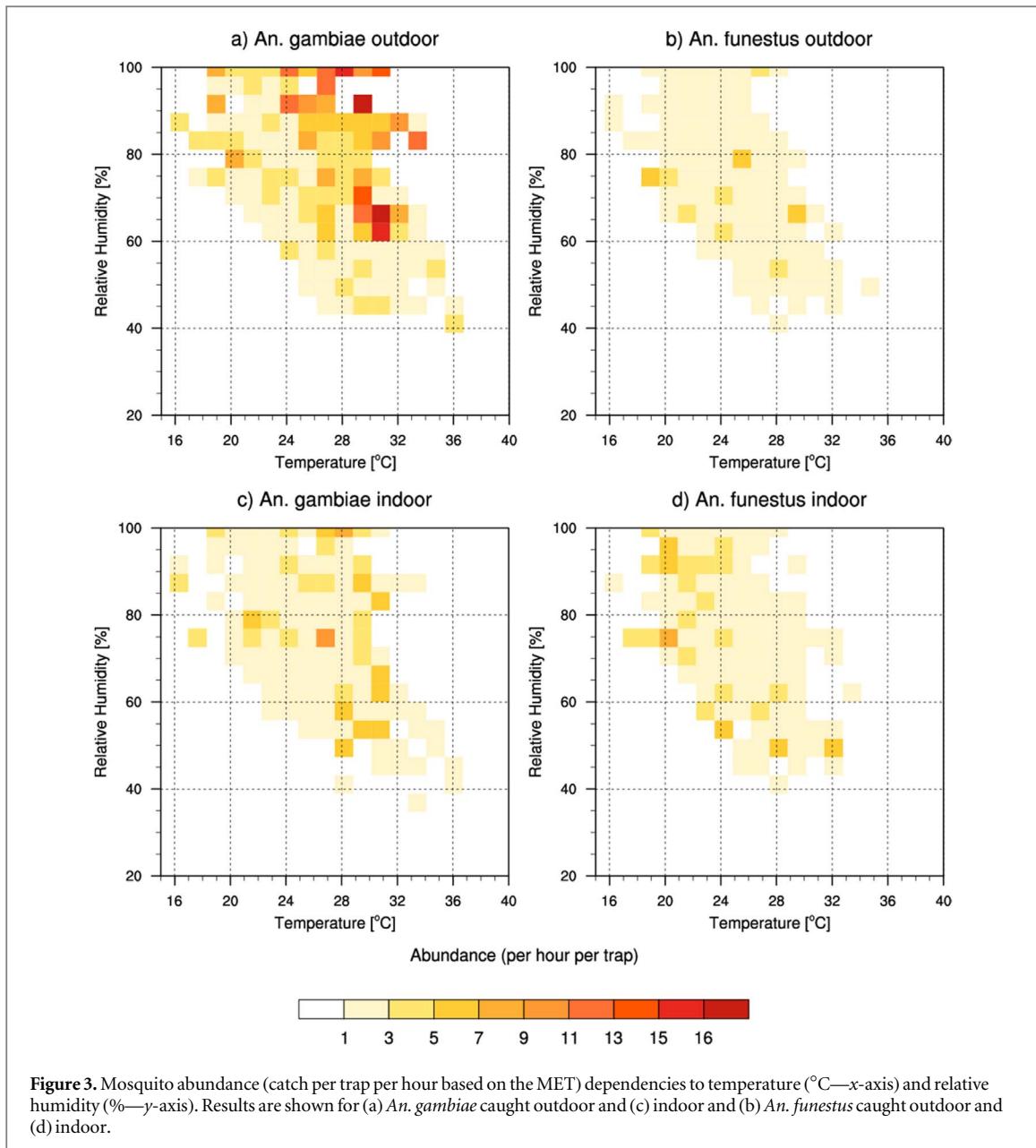


Figure 2. Comparison of (a) Nino 3.4 index (bars) and DMI index (solid line) ($^{\circ}\text{C}$), (b) rainfall (mm) and temperature ($^{\circ}\text{C}$) conditions for Ifakara (weather station data) for the period 2016–17. (c) Averaged *Anopheles* mosquito abundance for all villages (catch per trap per night based on CDC traps) for the same period.

population in the study area was not straightforward. However, we highlighted a robust relationship between the following La Niña, regional drought conditions and the crash of the vector population in the area. Such sudden and strong decline in mosquito numbers has not been observed in the region during years with normal dry season conditions (Ngovo *et al* 2017). The sudden decline was more pronounced for *An. funestus* which also consistently showed a more

limited tolerance to high temperature conditions than *An. arabiensis*. However, data was limited and baseline data was derived from information collected throughout the previous 3+ years only. Due to this relatively short, but high quality record, extended by our study, continuing to monitor mosquito dynamics would be beneficial.

Almost twice as many *An. arabiensis* as *An. funestus* were caught with all trap types. In line with other



studies, malaria vector populations showed strong seasonality (Koenraadt *et al* 2004, Ngowo *et al* 2017).

Notably, *An. arabiensis* numbers peaked in phase with rainfall, while *An. funestus* numbers were highest 2–3 months after the rainfall peak as seen in the previous year 2015 (Ngowo *et al* 2017). This is most likely related to their respective larval ecology—*An. funestus* develops much slower than *An. arabiensis* (Kirby and Lindsay 2009, Lyons *et al* 2013) and prefers still, clean, more permanent water bodies, while *An. arabiensis* happily breeds in temporary water bodies (Gillies and De Meillon 1968, Minakawa *et al* 1999, Charlwood *et al* 2000, Gimnig *et al* 2001). During the rainy season, breeding sites become turbid, while water bodies become an oasis of still and clean water during the dry season—making them highly attractive for oviposition and increasing the survival of *An. funestus*' offspring, increasing their density. Laboratory studies

also indicate a negative effect of temperatures above 28°C and fluctuating temperatures on *An. funestus*' larval development and adult survival (Charlwood 2017). The peak rainy season in Tanzania is associated with both, high temperature and temperature fluctuations.

In the Kilombero Valley region, overall temperature seems favourable year round for *Anopheles* and the relationship could not be interpreted between monthly changes in temperature and mosquito abundance, but it had a marked effect on the micro-climate level. At a local scale, higher temperatures inside houses were associated with decreased abundance of anophelines (table 2(a)). In our study, the highest temperature at which *An. funestus* were caught indoors was 32°C which is in line with published maximum threshold of survival for anophelines (Mordecai *et al* 2013, Ngowo *et al* 2017). *An. arabiensis*

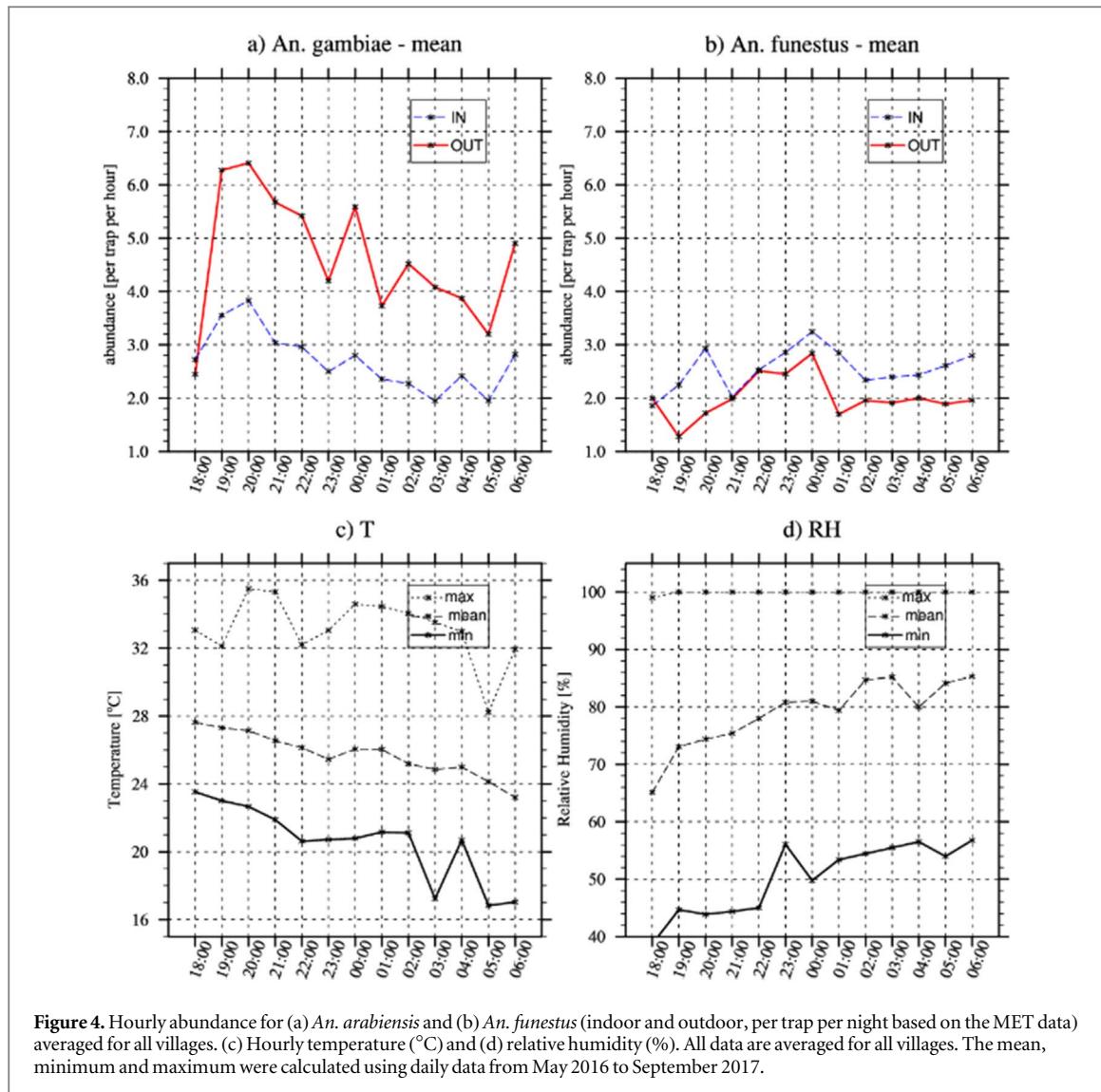


Figure 4. Hourly abundance for (a) *An. arabiensis* and (b) *An. funestus* (indoor and outdoor, per trap per night based on the MET data averaged for all villages. (c) Hourly temperature (°C) and (d) relative humidity (%). All data are averaged for all villages. The mean, minimum and maximum were calculated using daily data from May 2016 to September 2017.

proved to be more resilient to high temperatures and was even collected at 36 °C. Unsurprisingly, *An. arabiensis* numbers were positively associated with the wet season, while there was a negative relationship with maximum temperature. The apparently higher sensitivity to micro-climatic conditions by *An. funestus* was confirmed by our GLMM model showing negative associations with both minimum and maximum temperature. Other variables such as village, RH and saturation deficit did not seem to influence host-seeking mosquito abundance indoors, even though both populations decreased dramatically during the period of drought. The lack of significant effect of RH could point to the existence of thresholds which were not captured by our model type. The influence of micro-climate on the location of host-seeking vectors as measured by the METs, showed an increase of the proportion of anophelines caught outdoors during the wet season. *An. arabiensis* and *An. funestus* exhibited significant differences in their night-time host-seeking behaviour. *An. arabiensis* was caught at much higher numbers outdoors and in the early evening hours.

While indoor numbers gradually decreased throughout the night, outdoor numbers showed another peak at midnight. The majority of *An. funestus* on the other hand, was consistently caught indoors.

The known, more flexible behaviour of *An. arabiensis* (Fornadel *et al* 2010, Russell *et al* 2011, Gordicho *et al* 2014), including increased outdoor feeding earlier in the evening (Norris and Norris 2013, Kaindoa *et al* 2017a), has serious implications for the success of vector control. Mosquitoes that bite outdoors and earlier in the evening, before people get under their LLIN, as reported by other studies (Tirados *et al* 2006, Maliti 2016), tend to avoid the main control strategy used against them. On the other hand, *Anopheles funestus* was found to be highly endophilic in our study and this is confirmed by others (Gillies and De Meillon 1968, Pates and Curtis 2005, Lounibos 2007) which makes it more vulnerable to LLINs and most likely caused its decline in many areas after the introduction of control methods (Meyrowitsch *et al* 2011, Zhou *et al* 2011). With ENSO now occurring in a warmer background, due to

Table 2. The association of micro-climate variables and season for host-seeking *An. arabiensis* with (a) the predicted mean abundance per night per CDC light trap and (b) the estimated change in the exophily ('location' refers to indoor versus outdoors) and for host-seeking *An. funestus* with (c) the predicted mean abundance per night per CDC light trap and (d) the estimated change in the exophily. Only variables with a *p*-value below 0.05 are shown.

<i>An. arabiensis</i>				
(a) CDC light trap				
Variable	Max. indoor temperature	Wet season		
Coefficient	-0.197	6.87		
P-value	<0.0001	<0.0001		
Mean predictive estimate	1.64 (1.55–1.73)	2.72 (0.12–51)		
(+/-95% CI)				
(b) Mosquito electrocuting trap				
Variable	Location: wet season			
Coefficient	0.61			
P-value	<0.0001			
Mean predictive estimate	3.68 (2.87–4.73)			
(+/-95% CI)				
<i>An. funestus</i>				
(c) CDC light trap				
Variable	Min. indoor temperature	Max. indoor temperature		
Coefficient	-0.101	-0.113		
P-value	<0.05	<0.05		
Mean predictive estimate	1.8 (1.66–1.95)	1.78 (1.59–1.99)		
(+/-95% CI)				
(d) Mosquito electrocuting trap				
Variable	Location: wet season			
Coefficient	0.35			
P-value	<0.05			
Mean predictive estimate	2.85 (2.13–3.81)			
(+/-95% CI)				

climate change (Cai *et al* 2014), the impact of the warm El Niño phase may exacerbate malaria transmission, while the impact of the cold La Niña phase might reduce it over the region.

5. Conclusion

While the effect of El Niño could not be established in this study, La Niña caused drought at a regional scale which led to decreased mosquito abundance. In terms of micro-climate, our study confirmed that temperature and to a lesser extent RH has an impact on vector behaviour, with new control strategies for outdoor biting vectors early in the evening urgently needed.

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The authors declare no conflict of interest.

Data

The weather station data can be requested by contacting Mrs Fatuma Matwewe at the Ifakara Health Institute, Tanzania (fmatwewe@ihi.or.tz). The gridded climate data is publicly available online. The mosquito abundance data is publicly available on the NERC's Environmental Information Data Centre at <https://catalogue.ceh.ac.uk/documents/89406b06-d0aa-4120-84db-a5f91b616053>.

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